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SHOOTS OF PHYLLOSTACHYS NIGRA MUNRO

UNIV OF MICH

A study of the grand period of growth in bamboo

WILLARD M. PORTERFIELD, JR.

(WITH THIRTY-FOUR TEXT FIGURES AND PLATE 10)

The conception of the grand period of growth as applied to plants and plant parts was developed by Sachs (1874) to designate the total period of enlargement. It was called the 'grand period' in contrast to the small periodic oscillations of growth which on the grand curve would appear as smaller elevations and depressions. One of Sachs' original series of measurements was made on the terminal internode of a seedling of *Phaseolus multiflorus*. Elongation was found to begin slowly, then to become gradually more rapid and finally to attain a maximum, after which it slowed down and shortly ceased altogether as the part in question reached maturity. Sachs states that this procedure holds, not only for the separate zones of roots, internodes, and leaves, as well as for entire organs, but also 'for each single minute area of a young cell.' The grand curve drawn with the increment values as ordinates and the time intervals as abscissae is symmetrical. It commences with a gradual rise which becomes steeper as it reaches the maximum point, then in the same manner slopes downward to the x-axis again. His own work, together with that of Köppen and Hartig, to which he refers, demonstrates a persistent trend of growth rate during the grand period, despite climatic conditions. Measured at shorter intervals, however, much more variation of rate usually is evident and greater correlation with external factors of light, temperature, and moisture becomes apparent.

The grand period of growth covers not only the enlargement of some part already in existence, but the production of a fully formed organ or series of organs with definite parts and specific characters. Pfeffer says, 'The term growth may be used to indicate all formative processes leading to a change of shape or of structure.' Does this imply that morphogenesis

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is essentially a process of reorientation whereby building units, like particles of sculptor's clay, are thrust about here and there through the operation of a formative principle till a required shape is attained, or does it mean the working out out of an inherited plan through the activities of living protoplasm? In the light of present-day knowledge of the cell and of cell activities, it is hardly necessary to point out that the capacity for form development is a part of the heritage of any cell aggregate and that in actual expression it represents the activity of a specific cell protoplasm. Plant growth, organ enlargement, regional stretching and root elongation are manifestations of one and the same thing—cell activity as observed in cell-division, cell enlargement, and cell differentiation. Causal agents postulated as initiating, accelerating, and maintaining growth, therefore, should be studied in the light of their effects on the cell. Growth and morphogenesis in all grades of plants are inextricably linked, since during growth the response of cells to whatever stimulus takes place with direct reference to the nature and structure of the future organs. To such a study with reference to bamboo my work should serve as an introduction.

Among the problems that are most mooted among students of plant growth are the periodic changes in rate of growth, the dominance of the apical meristem, and the genesis of form. Various ideas have been advanced from time to time toward the solution of these problems. Sachs assumed that specific organ-forming substances were needed for growth and that the exhaustion of these substances in the growing regions was the cause of the inhibition of growth in dormant buds of a plant. Pfeffer (1900) postulated regulatory influences exerted by enzymes and other chemical substances. Erréra (1904) assumed inhibiting substances emanating from the terminal growing point. Loeb (1916) for *Bryophyllum* assumes that inhibition involves the transportation downward of chemical substances produced at the apex which prevent the development of secondary shoots while the terminal bud is elongating. Later he assumes that the inhibiting action of one plant part upon another is due to the fact that sap flows prevailingly toward the *Anlagen* that first begin to grow. Child and Bellamy (1920), also for *Bryophyllum*, assert that the physiological

dominance of a plant part is connected with its metabolic activity with the transmission of dynamic changes through the active protoplasm. Appleman (1918), working with potato sprouts, found that their vigor bears a direct relation to the size of the seed piece from the tuber. If the seed piece is small, weak shoots develop and remain weak despite optimum soil conditions, yielding only a small crop of tubers. Appleman criticized Loeb's assumption that precedence of growth determines flow of sap to one part, thus inhibiting the growth of another, on the ground that the apex could only have the effect postulated after it had begun to grow, and that it does not, therefore, explain initiation of growth. By cutting potato tubers transversely, he found that shoots developed from the basal segments, but when he cut them longitudinally the basal buds failed to grow. From these facts he assumes that the terminal buds dominate and exert an inhibiting influence on the basal laterals.

Pearsall (1923) does not find that it is necessary to assume the existence of special growth controlling substances. He attributes primary changes in rate of growth to relative food material from the roots. In regard to the data of Balls and Holton and of Harland on the curve of growth rate of cotton plants, he explains that the appearance of flowers curtails the growth of the stem apex and that the development of fruits reduces the rate of flowering because the supply of food material (nitrates) from the roots appears to be the limiting factor in the growth rate of the entire plant.

Smith (1924), in studies on the early growth rate of hyphae of *Botrytis cinerea*, found no evidence for the existence of special growth substances which insure the dominance of apical growth. He believes that a pressure gradient, in which higher concentrations of sap in regions behind the tip where interposing septa have made diffusion more difficult, determines the formation of a new branch to relieve the congestion. Summers (1924) investigated the cycle of shoot growth with reference to bud formation, the external and internal factors involved, and like Lewis and Tuttle (1923), who studied seasonal changes in leaf cells of *Picea canadensis*, finds that changes from the active to the resting condition in a bud, like the changes in the state of the chloroplasts from the winter to the summer condition,

are not bound up with temperature relations nor with variations in the quantity or quality of food reserves. The assumption of an inherent periodicity in life processes is suggested as responsible for all these cyclic effects.

Nevertheless there is evidence in plants of behavior during growth that seems to imply the effects of specific substances. Whether these substances are definite products of cell metabolism, or whether we are dealing all the while simply with combinations of indirect effects, is not yet known, but modern workers like Reed (1927) and others are postulating with conviction growth-promoting substances of intracellular origin and with characteristic properties. In the sense that the rate of growth is controlled through the interaction of the protoplast and compounds which it produces, the grand period of growth is then but an expression of specificity, and by its specificity we mean that aggregate of qualities in any variety of plant or animal which, as a total of consistently definable traits, distinguishes it from any other variety.

Robertson (1923) pictures growth as a process similar in operation to an autocatalyzed monomolecular reaction. Among other advocates of the chemical basis of growth, Penrose (1925), in showing the relation between growth rate and structure in plants, demonstrated autocatalytic retardation. The close agreement of the calculated results with those derived from actual observations of leaf outline and of periodicity in the size and arrangement of plant parts generally warrants the assumption of a gradient of growth-capacity, which first increases, then decreases, as the axis of growth is ascended. Reed (1927) touches very closely the problem of growth specificity in plants when he suggests that the various metabolic gradients may involve gradual changes in the nucleo-cytoplasmic ratio. Physiological activity, not accumulation, is emphasized as the condition which initiates growth.

I have studied the grand period of growth of bamboo with reference to the effect of climatic factors on the rate of growth and on rates of growth in different species. The external morphology of the bamboos is already fairly well known, but the physiology and internal anatomy have been barely touched, and the cytology not at all. I shall later report on an investigation of growth from the standpoint of cell differentiation and

histogenesis. My data cover the period from 1923 to 1926, inclusive. During this time I have kept careful records of temperature and moisture conditions, with specific notes as to light, wind, and rainfall.

REVIEW OF LITERATURE

As far as I have been able to find out, the first records of bamboo shoot growth were made by Mooty-Oollah, the Hindu head-gardener of the Calcutta Botanical Garden, in 1833. These were published fifteen years later by Martius (1848). Measurements were made twice daily but no notes or records of external conditions were kept. Four species were studied. *Bambusa gigantea* Wall. was found to grow 15.2 to 36.8 cm. daily and in thirty-one days 7.85 meters. Both *B. gigantea* and *B. arundinacea* Retz, of which only a few measurements were taken, grew faster in the night. *B. Balcoa* Roxb., on the other hand, grew from 6.3 to 22 cm. daily for twenty-three days and elongated more rapidly during the day. Too few measurements were made of *B. baccifera* Roxb. to draw any conclusions regarding the growth rate of this species.

The next investigator of any importance was Robert Scott (1849), who read before the Botanical Society of Edinburgh a paper entitled 'Remarks on the Growth of *Bambusa arundinacea* Retz.' The period of study was from August 19 to September 30, during which time the temperature was noted as having varied from 16.8° to 24.4°C. The daily growth between August 19 and September 1 averaged 19 cm.; from September 1 to 7, 55.9 cm.; and from September 7 to 30, 30.5 cm. The observations were made in the large conservatory at Chatsworth, England. Scott (1855) also observed several bamboos in Kew Gardens which became 20.7 meters high in five months. They appeared to grow very slowly until they reached a certain height, when they shot up 60 to 90 cm. in a day.

Fortune, during his explorations in China, 1843–1861, is reported as having measured shoots which grew 6 to 9 cm. in twenty-four hours. He intimated, furthermore, that growth was more active during the night than during the day.[1]

[1] The only reference to this observation of Fortune's has come to me through the work of the Messrs. Rivière. I have been unable to locate the exact passage in Fortune's book in which I thought it most likely to be, *Three Years in the Northern Provinces of China*, 1847.

Petermann (1860) reported that in the botanical garden at Edinburgh a species of bamboo grew 15.2 cm. a day at a temperature of 18.3–21.1°C. In Burma *Bambusa gigantea* was said to have reached 30.5 meters in height, and to have grown 45.7 cm. in twenty-four hours. But even this is surpassed by the report (Petermann, 1860) from Bengal of the growth of *Bambusa Tulda* Roxb., which in a month's time grew to a height of 21.3 meters, averaging 2.5 cm. an hour.

According to Messrs. Rivière (1878), Dr. Karl Koch reports that Inspector Bouché at the Berlin Botanical Garden observed that *Bambusa verticillata* Willd. grew 11 meters between August 22 and November 24, the range of variation in daily rate amounting to from 2 to 4 cm. The fastest rate of growth recorded for twenty-four hours was 22 cm.

In 1868 began the most careful series of investigations yet made. A. and C. Rivière (1878) for eight years had observed several of both the spring-growing and autumn-growing types of bamboos in the garden of the Hamma in Algiers. The initial rate of growth was found to be very slow. Following this, however, a gradual increase in the daily rate was noted until it exceeded 50 cm., after which it decreased steadily as the culm completed its height. It was found that the autumn-growing species, *Bambusa macroculmis* A. & C. Riv., *B. vulgaris* Wendl., and *B. vulgaris vittata* A. & C. Riv., grew more rapidly at night and that the maximum rate per twenty-four hours was less than that of the spring-growing species. Of the latter, *Phyllostachys viridi-glaucescens* A. & C. Riv., *P. nigra* Munro, and *P. aurea* A. & C. Riv. showed more rapid growth during the day. *P. mitis* A. & C. Riv., though belonging to this group, grew more rapidly at night, thus providing an exception which in the minds of the investigators tended to cast doubt on the existence of any relation between environmental factors and daily growth periodicity in bamboo. The maximum growth in twenty-four hours was that recorded of *P. mitis*, which was 50 cm. Very complete data as to temperature, relative humidity and general weather conditions were supplied by the meteorological station in Algiers.

Munro (1868), in his comprehensive monograph on the bamboos, makes only the barest mention of their growth rate.

Two and a half lines devoted to it are to the effect that there is a specimen of *Bambusa vulgaris* preserved in the British Museum which is stated to have grown 12.2 meters in 40 days at Chatsworth.

Dingler (1881), in the Palm House of the Botanical Gardes at Munich, observed a daily growth of 8 to 9 cm. Doubtlesn this was for *Bambusa vulgaris*, the same species which, according to the director of the Frankfurt Palm Garden, Herr Siebert, grew to a height of 16 meters in three and a half to four months' time, the greatest daily growth being 15 to 20 cm. Dingler himself made very careful measurements of internode length and width and discovered the fact that all internodes with the exception of those below the bud region tend to taper in their upper portion—*i. e.*, the diameter of the upper part is less than that of the lower.

The giant bamboo, *Dendrocalamus giganteus* Munro, was studied in Java by Kraus (1895). Daily measurements of growing shoots were taken in the Buitenzorg Gardens, beginning on November 13, 1893, and ending on January 13, 1894. He reported that temperature and weather conditions were almost constant, though no actual record of these conditions was kept. The maximum growth in twenty-four hours was 57 cm., or an average hourly growth of 2.37 cm. In sixteen cases, with one exception, growth was more rapid in the night. Despite the constancy of the weather conditions, his measurements showed great irregularity of growth from day to day. On one day it was 57 cm., on the next only 3; it was 41 cm. on another, followed on the next day by 12, and so on. Lovink (1890), a contemporary of Kraus, working wlth a species of *Dendrocalamus* in Ceylon during the months of February and March, noted the same sort of oscillations in rate of growth. Kraus claimed that these irregularities were unexplainable by environmental factors, such as temperature, humidity, and rainfall, and that the cause must lie in the culm itself.

Shibata (1900) gave the growth records of six culms of *Phyllostachys mitis* for three weeks in April to May, with daily notations of temperature and relative humidity. The records show the character of the grand period, but its relation to external factors is not discussed. Lock plotted the curves

from these data and found that they exhibited only slight general agreement with the curve of humidity. They parallel much more closely the variations of temperature.

The studies of Lock (1904) on the growth of giant bamboos, with special reference to the relation between conditions of moisture and the rate of growth, are without doubt the most carefully planned and carried out of any up to his day. The chief species under observation was *Dendrocalmus giganteus* Munro, but two others (*Gigantochloa aspera* Kurz, and *Bambusa spinosa* Roxb.) were also studied as checks. The study was made in the Royal Botanical Gardens at Peradeniya, Ceylon. The observations extended over a period of fifty-five days, June 20 to August 13, 1903. Several shoots of each species were measured daily, and the temperature, relative humidity, and rainfall were noted. The temperature was found to be very constant, the daily mean varying between 23° and 26°C., but the rainfall varied. The greatest observed growth of *D. giganteus* in twenty-four hours was 46 cm., and the variations in the daily rate of growth showed striking agreement with the variations in rainfall. The observations on *Gigantochloa* and *Bambusa* show the same relations. They tend to show, moreover, that the response of taller shoots is more marked than that of shorter ones. An investigation of the location and extent of the growing region of the shoot showed that in the most active period of elongation the growing region in the giant bamboo extends as far as 6 meters behind the growing apex, but in the beginning and toward the end of the grand period the region of elongation is much shorter. In the two cases investigated, growth was more rapid during the night. The ratio in the case of *Dendrocalamus* was 1.8:1, while in the case of *Gigantochloa* it was 3:1. Hourly growth was also investigated with a view to establishing its relation to the conditions of moisture. Oscillations in hourly growth seemed likewise to vary in accordance with changes in the percentage of moisture in the air. Among the factors governing growth, light was not considered of importance. Temperature was regarded as a minor factor in the regulation of growth rate. Conditions of moisture were given the place of paramount importance. The intermediate agency in bringing about response to varied conditions of moisture was thought to be the rate of transpiration

of the older culms of the plant. In other words, dry weather tended to accelerate transpiration to the extent that turgor pressure in the shoots was lessened and elongation thereby retarded.

Brown and Fischer (1918) of the Bureau of Forestry of the Philippine Islands made an economic survey of Philippine bamboos, and among other things studied their growth rates. Beginning with 1912 measurements had been made by the ivision of Investigation of the Bureau of Forestry, the most extensive series being that of ranger Oro in 1915. Brown and Fischer cite the records of three species, *Bambusa spinosa* Roxb., *B. vulgaris* Schrad., and *Gigantochloa levis* (Blanco) Merr., all of them tall forms, but the measurements were weekly, not daily. No records of rainfall, relative humidity, or temperature are reported and no information is given regarding daily periodicity. The culms of *B. spinosa* and *B. vulgaris* started to grow during the latter part of the dry season, but made very slow progress until the rainy season (July, August), while *Gigantochloa levis* started about the beginning of the rainy season. The most rapid growth usually took place in the latter part of the rainy season. The fastest rate recorded was 3.17 meters in a week made by *B. spinosa*, or 45 cm. a day. It is possible that the maximum at some time within the week may have been higher.

Osmaston (1918) measured the growth of *Dendrocalamus giganteus* in India. Measurements were taken twice daily from August 19 to September 11. When the shoots had attained an inconvenient height, the measurements were stopped, though they had not yet attained one-half of their mature height. By the middle of November one of them stood 21.6 meters. The most rapid growth recorded was 33 cm. in twenty-four hours. The curves of rainfall and maximum and minimum temperatures appear, but no growth curves are given for comparison. Night growth was about twice as rapid as day growth. Neither light nor temperature are put forward as causes of this difference. On the other hand, Osmaston asserted that the maximum growth rate was attained when the relative humidity was highest.

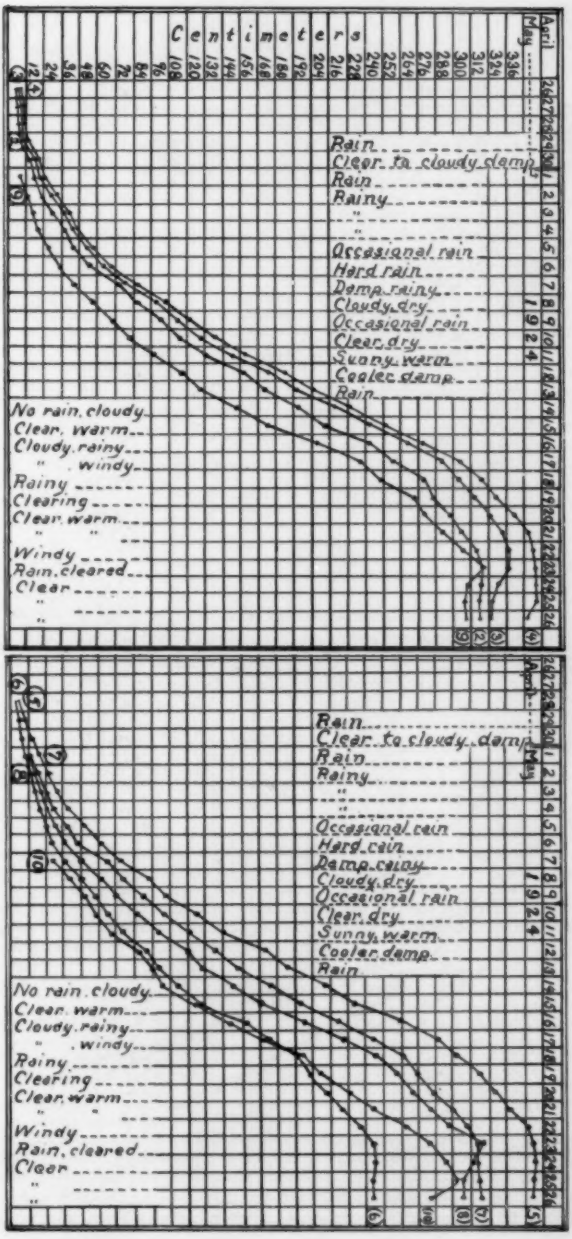
Galloway (1925) cites the work of Thomas in 1921 on the growth of *Phyllostachys bambusoides* Sieb. & Zucc., at the Chico Plant Introduction Garden. The greatest growth took place

during the day. The maximum increase for a twenty-four-hour period was 91.4 cm. The total time required for a culm 12.2 meters high to complete its growth including branches and leaves was found to be five or six weeks. Nothing as to external conditions during the period is mentioned.

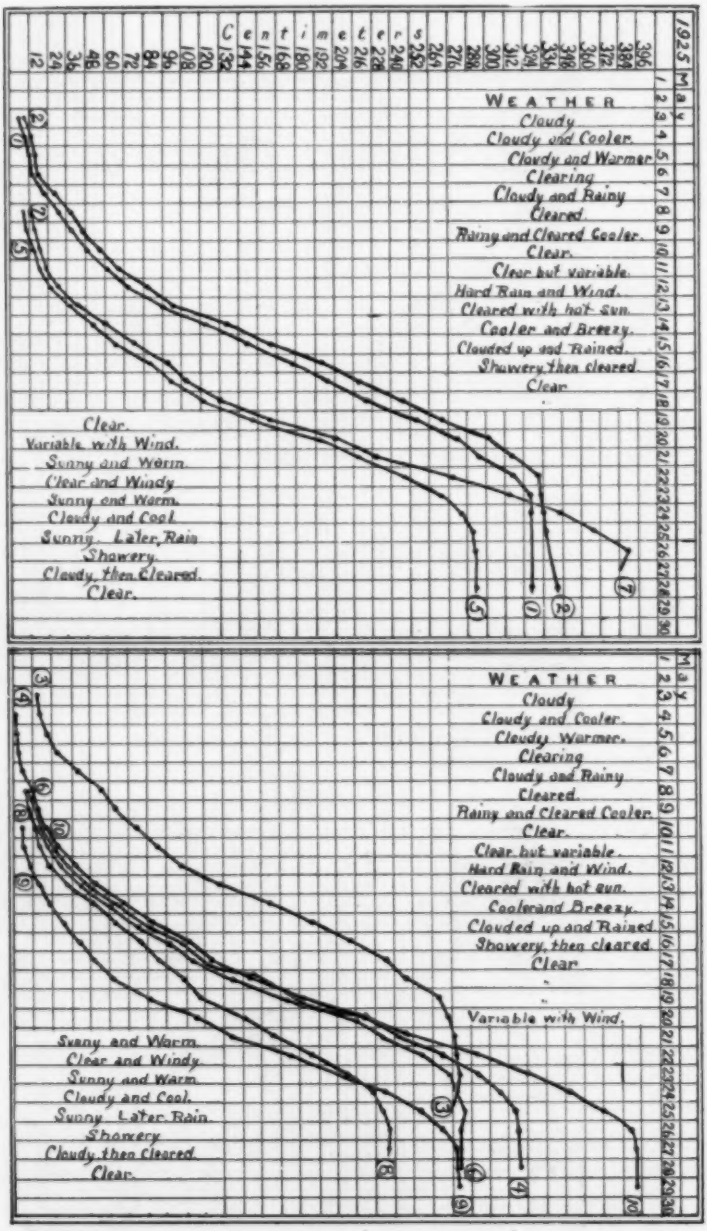
MATERIALS AND METHODS

Measurements of growing bamboo shoots were made on the campus of the St. John's University, Shanghai, China, in the years 1923 to 1926, inclusive. As the records for 1923 were incomplete, the discussion of them has been omitted. The two species studied were *Phyllostachys quadrangularis* Rendle and *Phyllostachys nigra* Munro, both of them comparatively small species in that part of the country. The former is an autumn-growing and the latter a spring-growing species. Measurements were made every morning at nine o'clock during the spring seasons of 1924, 1925, and 1926, and during the autumn seasons of 1925 and 1926. The former came in the months of April and May, the latter in October and November. It was thought that in choosing one each of the seasonal types interesting and significant comparisons could be made. Neither form studied is a clump-forming species, the culms all springing from the nodes of extended subterranean rhizomes.

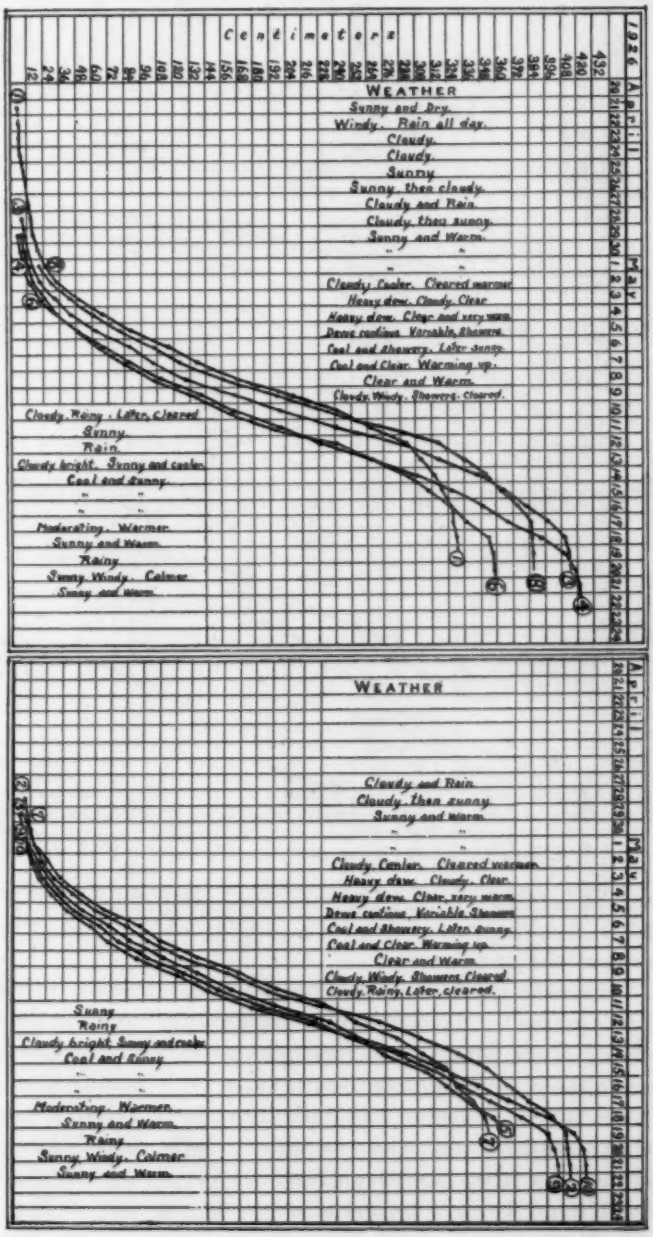
Because of the fact that I was dealing with small species, I did not have the difficulties encountered by Kraus and Lock in their work with the giant bamboos, and consequently avoided the chances of error involved in measuring the slender overhanging tips of nearly grown shoots. The equipment and method of measuring which I used was very simple. By attaching together two meter sticks end to end a measuring rod was obtained that was almost adequate in itself for the Square bamboo, though necessitating the aid of a step-ladder for the Black. The conical point made by the overlapping sheathing leaves embracing the growing apex served as an indicator while the shoots were still very young, but as they elongated this became no longer practicable, for the spine-like pseudophyll surmounting each sheathing leaf gives way on successively higher ones to leaf-like laminae that droop over (plate 10). I then followed the example of Messrs. Rivière and used the collar-like ligule at the juncture of pseudophyll and sheath as the indicator as



Figs. 1, 2. Grand period curves of *Phyllostachys nigra* 1924 shoots 2–10.



Figs. 3, 4. Grand period curves of *Phyllostachys nigra* 1925 shoots 1–10.



Figs. 5, 6. Grand period curves of *Phyllostachys nigra* 1926 shoots 1–10.

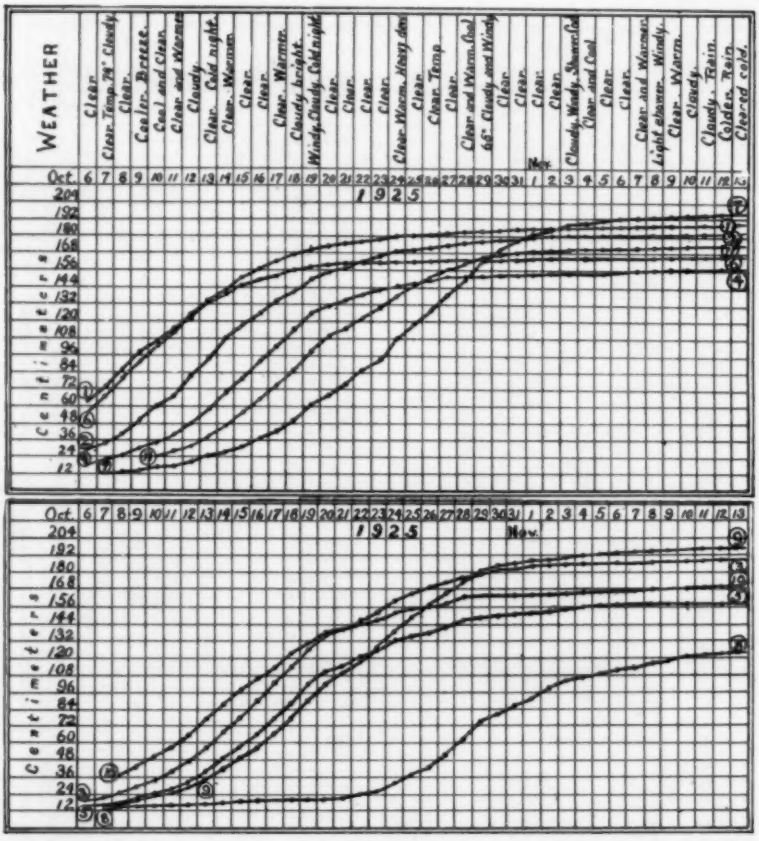
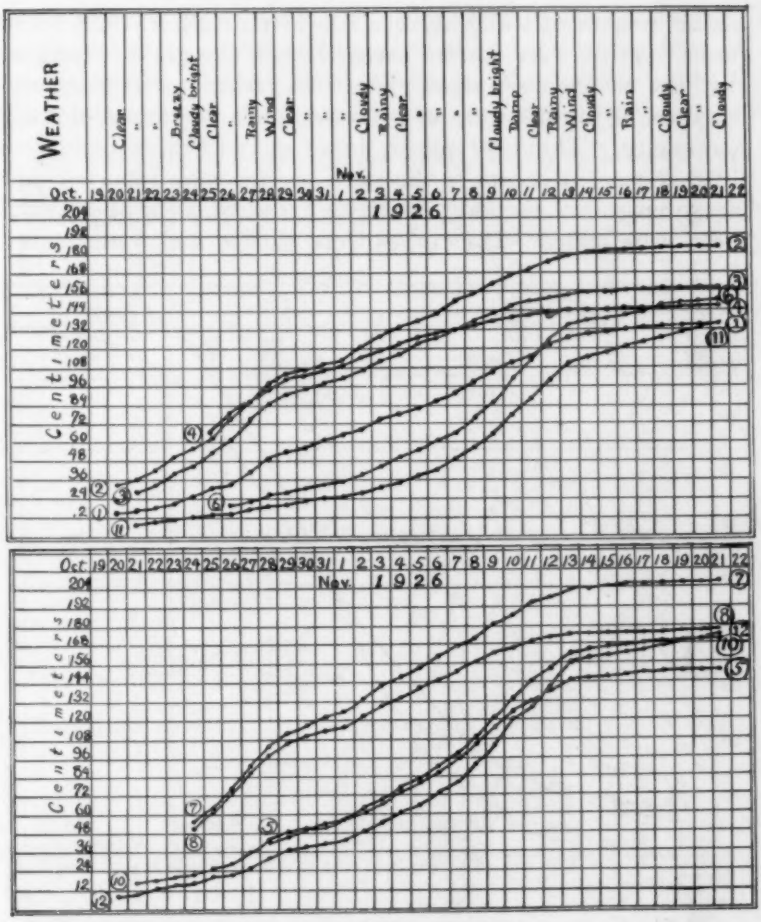


FIG. 7, 8. Grand period curves of *P. quadrangularis* 1925 shoots 1–11.

long as it remained the topmost one. As soon as it was superceded by the one lying next underneath, then the latter became the indicator.

The daily growth records are given in tables 1–5 (Appendix of this paper). Two columns are devoted to each shoot, the left-hand one for the measurement as taken and the right for the increase made during the previous twenty-four-hour period. These tables also give the daily records of relative humidity, mean temperature, and rainfall, which have been kindly checked by the Siccawei Observatory. Growth curves, to which reference will be made in a later section of this paper, were plotted from these data.



Figs. 9, 10. Grand period curves of *P. quadrangularis* 1926 shoots 1–12.

DATA AS TO GROWTH RATE IN PHYLLOSTACHYS QUADRANGULARIS AND P. NIGRA

In preliminary papers (Porterfield, 1925, 1927) on the growth of bamboos in China, particularly at Shanghai, I showed that oscillations in the rate of growth which occurred simultaneously in all shoots under observation were due to external conditions, and that chief among these varying external conditions was temperature. The earlier report contained an account of the growth of three culms of *Phyllostachys quadrangularis*, the

measurements of which were made in the fall of 1923. The measurements were started rather late in the grand period so that the curves were incomplete. No records of atmospheric moisture or rainfall were kept and no note was taken of daily periodicity. The 1927 paper, however, was more complete. Further measurements of the same species were reported and measurements of shoots of *Phyllostachys nigra*, a spring-growing form, were added. The curves were plotted and were related

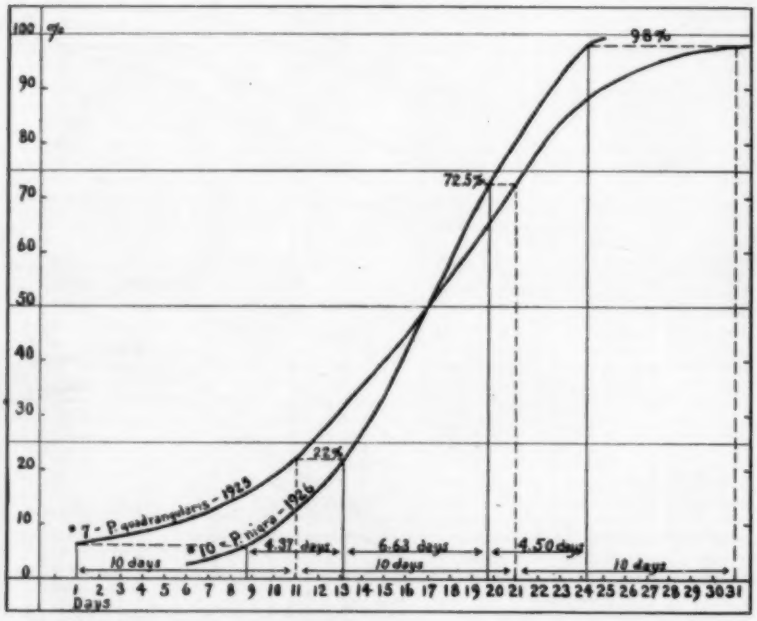


Fig. 11. A comparison of growth curves based on daily measurements in percentage of the total height.

to the accompanying data on thermic and psychrometric conditions. Daily periodicity was also investigated. In neither account, however, was the relation of growth rate to species difference discussed. The complete data from these measurements, except those of 1923, are included in tables 1–5 (see Appendix).

Beginning on April 26, 1924, ten shoots of *P. nigra* as they appeared above the ground were selected and measured daily

until May 25, when elongation had practically ceased (table 1). In the following spring, beginning on May 3 and ending May 28, ten more shoots of the same species were measured (table 2). In the autumn of that year I began a series of observations on

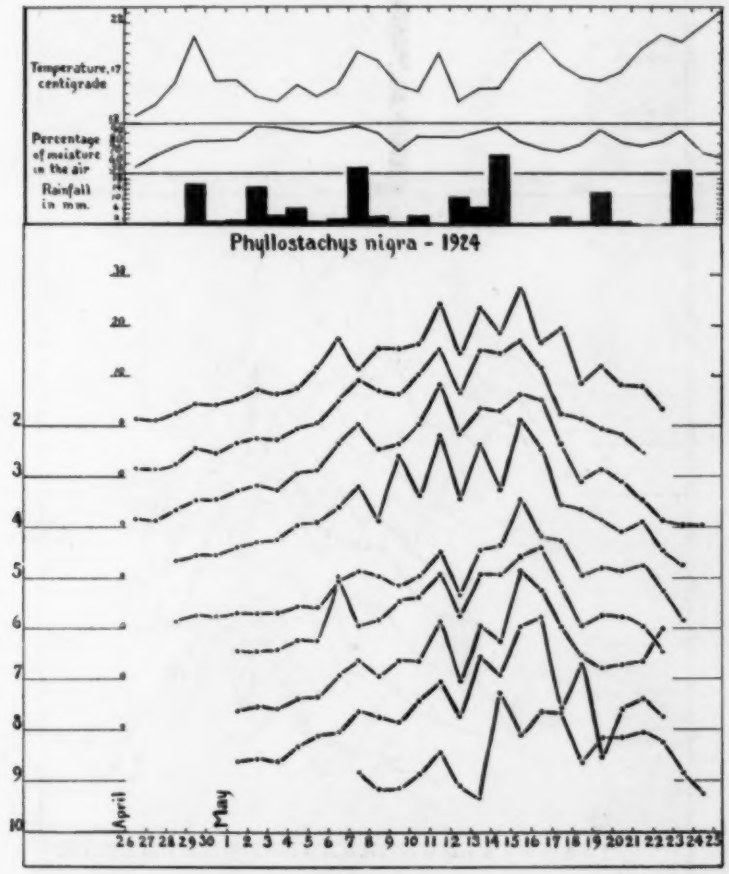

Temperature, in centigrade
Percentage of moisture in the air
Rainfall in mm.
Phyllostachys nigra - 1924
April
May
26 27 28 29 30 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25

Fig. 12. *P. nigra* 1924 shoots. The curves of daily growth with those of mean daily temperature, relative humidity, and rainfall.

Square bamboo, *Phyllostachys quadrangularis*. Accordingly on October 6, 1925, eleven shoots were tagged and measurements were taken until November 13 (table 4). In the spring of 1926 the last series of measurements of *P. nigra* were made. They

began on April 21 with one shoot, which by May 1 had been increased to ten, and were completed May 21 (table 3). The first of twelve shoots of *P. quadrangularis* started growth Octo-

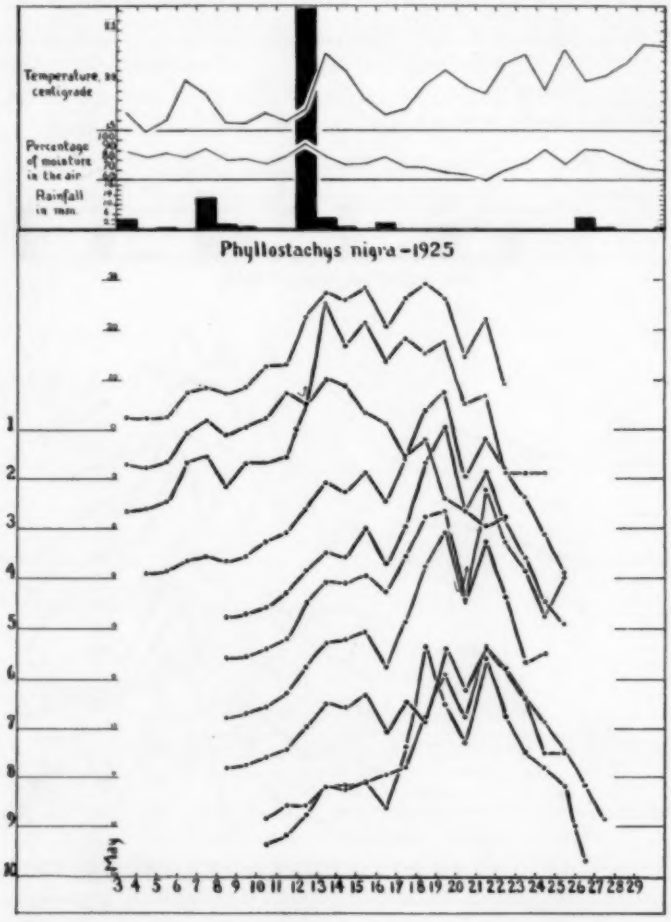


Fig. 13. *P. nigra* 1925 shoots. The curves of daily growth with those of mean daily temperature, relative humidity, and rainfall.

ber 20 of the same year, and by November 21 all had about ceased to grow (table 5). It should be stated that when the Black bamboo shoots had nearly ceased to elongate, their whip-like tips were quite frequently blown about and many times

broken or otherwise injured, thus terminating the measurements.

In looking over the tables of measurements, it becomes at

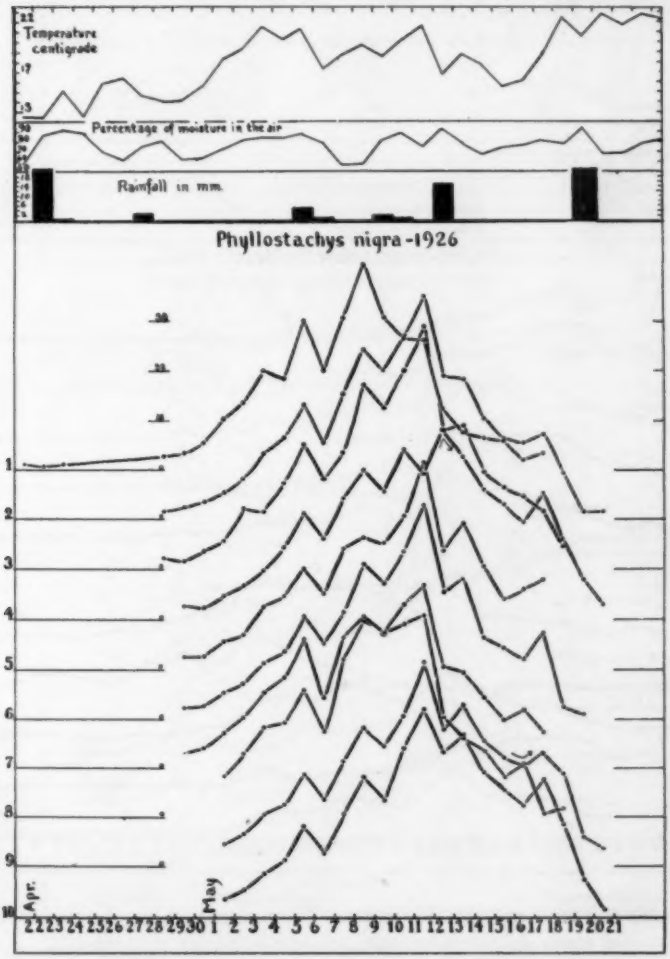

Temperature centigrade
Percentage of moisture in the air
Rainfall in mm.
Phyllostachys nigra-1926
Apr.
May
22 23 24 25 26 27 28 29 30 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21

Fig. 14. *P. nigra* 1926 shoots. The curves of daily growth with those of mean daily temperature, relative humidity, and rainfall.

once apparent that none of them begin at less than 4 cm., and generally at more. One never knows at just what spot a shoot is going to appear, so that in most cases before one is aware of

it a conical point has thrust up a few centimeters behind a nearby culm or beneath some leaves. There is always the question too of selection. I have chosen the most vigorous looking shoots as likely to be nearer the norm for the species, since

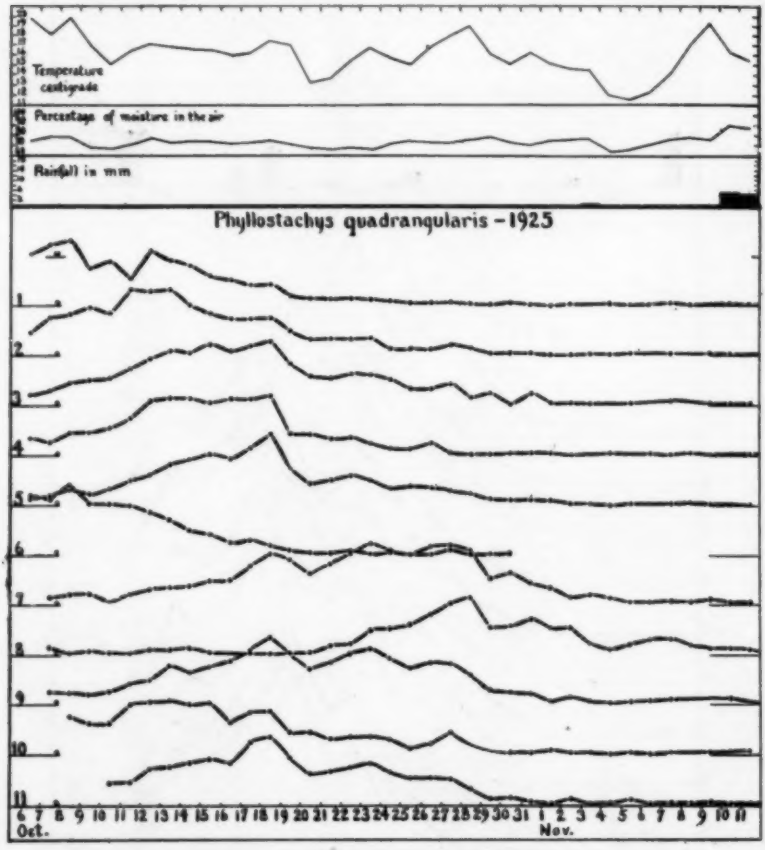


Fig. 15. *P. quadrangularis* 1925 shoots. The curves of daily growth with those of mean daily temperature, relative humidity, and rainfall.

farther south both species grow taller and thicker than they do in Shanghai. They must become fully observable, therefore, before it can be ascertained whether or not they are typical.

An observation of great interest is the amount and sequence of daily gain. It is noteworthy that the amount of this gain is

not constant but varies, and that it varies in a very definite way. In every shoot of both species the daily increase at first is very small, then it becomes larger until it reaches a maximum.

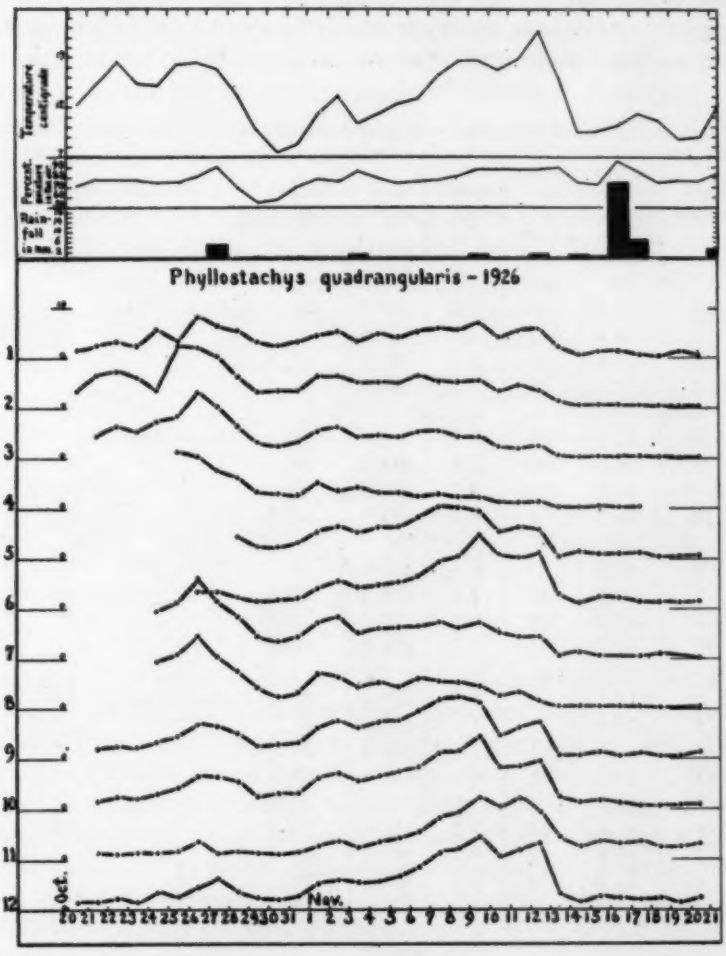


Fig. 16. *P. quadrangularis* 1926 shoots. The curves of daily growth with those of mean daily temperature, relative humidity, and rainfall.

The maximum rate is not reached by all shoots simultaneously, but at different times, depending on the date when elongation commenced. A comparative survey of the tables will show this.

The same thing is apparent in Brown and Fischer's (1918) table containing measurements of Philippine bamboos. After the maximum is reached, the growth rate begins to diminish and soon reaches the zero point. The general trend of the growth rate is seen most clearly in figures 12–16, in which the curves are based on the daily increment. It is very noticeable

TABLE 6

Analysis of growth measurements with special reference to time of maximum growth rate

SHOOT NUMBER	MAXIMUM GROWTH IN 24 HOURS		GROWTH IN FIRST DAY	FINAL HEIGHT	TOTAL TIME	SPECIES AND YEAR
	Amount	Time				
	cm.	*days*	*cm.*	*cm.*	*days*	
4	28.4	16	1.6	358.0	30	P. nigra, 1924
5	28.4	13	3.1	357.0	27	" "
8	31.8	15	3.6	319.8	23	" "
9	32.2	15	3.5	321.0	23	" "
4	37.9	15	1.0	319.0	23	" 1925
5	40.8	11	2.8	293.0	19	" "
7	48.8	13	2.2	390.0	19	" "
10	46.5	8	6.2	393.0	18	" "
2	45.5	13	1.6	413.0	24	" 1926
3	49.5	13	2.0	414.5	22	" "
6	43.0	12	2.1	359.0	22	" "
10	42.5	11	3.9	424.0	21	" "
2	13.7	5	4.9	183.3	39	P. quadrangularis, 1925
5	14.4	12	1.1	159.5	38	" "
6	14.0	2	12.0	166.8	39	" "
11	13.9	8	4.1	174.4	35	" "
6	15.0	14	3.7	150.6	27	" 1926
7	16.3	2	9.9	207.1	29	" "
8	14.8	2	9.7	178.5	29	" "
12	14.6	20	1.3	173.6	33	" "

from the tables that the rise and fall of growth rates is quite different for the two species which I studied. The same figures emphasize this difference also. Whereas the curves in figures 12, 13, and 14 rise quickly to high maxima, those in figures 15 and 16 are very flat comparatively, but within each species the curves all have a similar character.

The tables are consistent in showing that the shoots of *P. nigra* grew to be taller on the average than those of *P. quadrangularis*, and this is a difference which is consistent throughout. The daily increment of *P. nigra* is also consistently higher than that of *P. quadrangularis*, which has a longer growth period. It requires only 19 to 25 days for *P. nigra* growing in the wet season of spring to complete an elongation which results in a relatively tall culm, whereas it takes from 29 to 37 days for *P. quadrangularis* growing in the dry season of autumn to reach its much lower height (table 7). All individual shoots of the same species have a grand period of similar extent in time and a curve of similar form. The tall culm

TABLE 7

Average rate of growth for shoots of P. nigra, spring-growing, and P. quadrangularis fall-growing, calculated on the basis of the data of table 6

SPECIES	YEAR	AVERAGE HEIGHT	AVERAGE TIME	AVERAGE RATE PER DAY
		cm.	*days*	*cm.*
P. nigra	1924	338.0	25	13.0
"	1925	348.0	19	17.8
"	1926	402.6	22	18.4
P. quadrangularis	1925	171.0	37	4.5
"	1926	177.4	29	5.9

and the short culm, as nos. 10 and 3 of *P. nigra* in 1925 (fig. 4), show relatively the same characteristic rates of growth (table 10). Those of different years, although growing as they did under varying external conditions, have the same habit. The average height of the 1926 culms of *P. nigra* is greater than that of the 1925 group, which is in turn taller than that of the 1924 culms. The same differences, though less pronounced, are shown by the culms of *P. quadrangularis*. A discussion of these differences in height will be taken up in the section on the relation of external factors to growth rate.

The slope of the grand period curves is another characteristic to note. The graphs of all shoots of the Black bamboo, of different years and of various sizes, show in general a certain degree of slope, while those of the Square bamboo have a slope that is much less steep. The slope of the curves is of course

TABLE 8

Measurements of a typical culm of P. nigra and of P. quadrangularis with special reference to relation between length of internode of mature culm and growth rate in shoot no. 4, 1925, P. nigra, and no. 9, 1925, P. quadrangularis[a]

PHYLLOSTACHYS NIGRA					PHYLLOSTACHYS QUADRANGULARIS				
Typical old culm Full height, 324.0 cm.			Shoot no. 4, 1925 319.0 cm.		Typical old culm Full height, 200.0 cm			Shoot no. 9, 1925 196.7 cm.	
Internode	Length	Total above ground	Daily gain	Daily measurement	Internode	Length	Total above ground	Daily gain	Daily measurement
	cm.	cm.	cm.	cm.		cm.	cm.	cm.	cm.
									16.1
								2.5	18.6
				1.4	1	3.6	3.6	2.4	21.0
			1.0	2.4	2	5.9	9.5	2.0	23.0
			1.6	4.0	3	7.9	17.4	2.8	25.8
			3.7	7.7	4	8.9	26.3	4.2	30.0
			4.3	12.0	5	9.4	35.7	5.0	35.0
			3.7	15.7	6	9.8	45.5	8.0	43.0
1	?	5.0	4.5	20.2	7	9.9	55.4	6.7	49.7
2	10.2	15.2	7.4	27.6	8	9.8	65.2	7.8	57.5
3	13.4	28.6	9.4	37.0	9	9.4	74.6	9.0	66.5
4	16.3	44.9	14.0	51.0	10	9.0	83.6	11.3	77.8
5	19.4	64.3	19.3	70.3	11	8.7	92.3	13.7	91.5
6	20.4	84.7	17.7	88.0					
7	20.4	105.1	21.5	109.5	12	8.5	100.8	10.5	102.0
8	19.0	124.1	15.5	125.0	13	8.3	109.1	7.6	109.6
9	19.3	143.4	24.0	149.0	14	8.2	117.3	8.8	118.4
					15	8.1	125.4	10.6	120.0
10	18.7	162.1	34.5	183.5	16	7.8	133.2	11.4	140.4
11	19.2	181.3	37.9	221.4	17	7.6	140.8	9.6	150.0
12	17.7	199.0	20.6	242.0	18	7.5	148.3	7.7	157.7
13	17.3	216.3	28.5	270.5	19	6.9	155.2	8.8	166.5
14	15.6	231.9	22.1	292.6	20	6.9	162.1	8.5	175.0
15	15.0	246.9	16.4	309.0	21	6.9	169.0	6.0	181.0
16	12.3	259.2	9.0	318.0	22	6.6	175.6	3.0	184.0
17	11.9	271.1	1.0	319.0	23	5.9	181.5	2.8	186.8
18	9.8	280.9			24	5.4	186.9	2.2	189.0
19	7.8	288.7			25	4.3	191.2	0.8	189.8
20	7.1	295.8			26	2.8	194.0	1.7	191.5
21	5.9	301.7			27	2.0	196.0	0.8	192.3
22	4.9	306.6			28	2.0	198.0	0.3	192.6
23	4.0	310.6			29	1.0	199.0	0.6	193.2
24	3.7	314.3			30	1.0	200.0	0.8	194.0
25	4.1	318.4						1.0	195.0
26	3.0	321.4						....	.....
27	2.0	323.4						....	.....
28	0.6	324.0						1.2	196.2
								....	.....
								0.1	196.7

[a] Cross rule indicates half height.

indicative of the rate of growth expressed in centimeters per day—a steep curve means rapid growth, a flat one slow growth. While the Black bamboo shoots reach a maximum rate of 28.4 to 49.5 cm. per day (table 6) and have an average rate per day of 13 to 18.4 cm. (table 7), the Square bamboo only attains a maximum rate of 13.7 to 16.3 cm. per day and an average daily rate of 4.5 to 5.9 cm. The difference in relative growth rates is fully brought out by the comparison shown in figure 11, in which the relative growth of a shoot of each species in percentage of total height is plotted against time. To compare the rates let us consider the period of time required by each of the shoots in figure 11 to grow equivalent amounts. We may consider 6 per cent of the total height as the beginning point; this is reached after 1 day by *P. quadrangularis* and after 8.75 days by *P. nigra*. Thus 1 day may be taken as zero time for the former and 8.75 as zero time for the latter. *P. quadrangularis* reaches 22 per cent of its total height 10 days later, but it takes *P. nigra* only 4.37 days to attain the corresponding height. *P. quadrangularis* reaches the 72.5 per cent point 10 days later, whereas *P. nigra* requires only 6.63 days to reach the same point. After 10 more days *P. quadrangularis* comes up to the 98 per cent mark, which is reached by *P. nigra* after only 4.50 days. Thus it takes 30 days for *P. quadrangularis* to grow from the 6 per cent point to the 98 per cent point, but it takes *P. nigra* only 15.50 days to make the corresponding growth.

As noted above, these two Shanghai bamboos grow at different seasons, *P. nigra* in the spring (April and May) and *P. quadrangularis* in the autumn (October and November). This difference in season of growth in length is an evidence of specificity, possibly in the same category as that of periodical flowering. This relation will be considered further in the discussion. Ony may observe from the record of climatic factors that autumn in general is a comparatively dry season at Shanghai. In 1925 there were only four days of rain during the period of measurement, three of which came in succession at the very end, and in 1926 nine, on one of which it rained 30.3 mm. The spring, on the other hand, is usually quite a wet season. In 1924 there was some precipitation in twenty of the days on which measurements were being made. On seven of them

there were over 10 mm. of rainfall. In 1925 twelve days were rainy, with two of them over 10 mm. and one 89.9 mm. The year 1926 was drier, as indicated by only nine days with any rain, only two of which recorded over 10 mm. The relative humidity in the autumn during the growing season varied in 1925 between 64 and 90 per cent, averaging about 75 per cent. In 1926 the atmospheric conditions were less dry, the range being 54.9 to 96.8 per cent, and average about 78 to 81 per cent. In the spring growing season the relative humidity is a little higher. In 1924 the range was 56 to 97 per cent, average

TABLE 9

Analysis of growth measurements with reference to the height from the ground at which shoots of P. nigra and P. quadrangularis of ultimate heights 324.0 cm. and 200.0 cm., respectively, reach their maximum rate

SPECIES AND YEAR	SHOOT	MAXIMUM RATE	FROM HEIGHT	TOTAL HEIGHT
		cm.	cm.	cm.
P. nigra, 1924	2	27.4	213.4	319.6
" "	8	31.8	168.0	319.8
" "	9	32.2	205.1	321.5
" 1925	1	28.7	150.5	329.0
" "	4	37.9	183.5	319.0
" 1926	1	41.2	168.7	331.4
P. quadrangularis, 1925	1	13.2	86.0	189.5
" "	7	12.5	95.5	196.0
" "	9	13.7	77.8	196.7
" 1926	7	16.3	76.5	207.1

85 to 92 per cent; in 1925 the range was 60 to 97 per cent, with an average of 80 to 89 per cent; and in 1926 the range was 58 to 93 per cent, average of about 75 per cent.

The mean daily temperature in the fall ranges between 7.5° and 19.6°C. In 1925 the average during the period from October 6 to November 11 lay around 14° to 16°, while in 1926 from October to November 21 it was lower, being around 10° to 12°. For the vernal bamboo, temperature conditions averaged considerably warmer. For the period from April 26 to May 25, 1924, the temperature variation ranged between 12° and 21°C., average about 15° to 17°; for the period May 2 to 30, 1925, 14.9° to 23.5°, average 18° to 21°; and for the period April 21 to May 23, 1926, 12.4° to 22.7°, average 17°

to 18°. These are records only of mean daily conditions and give no information as to the fluctuations during the day, which I know to be quite marked.

The lack of data as to hourly oscillations in atmospheric conditions is felt particularly when we consider daily periodicity in growth rate. The daily rhythm of the growth rate is as characteristic of the species as its seasonal periodicity, and the external conditions under which it expresses itself should be known in order to understand its relation to them. The table of average hourly rates of growth for shoots 1 and 5 of *P. nigra* in 1926 (table 11) reveal quite clearly the nature of the oscillations in rate of elongation during the alternate periods of day and night. The twelve shoots of *P. quadrangularis* were measured twice daily for only five days (table 12) so that the data for studying the relations of nocturnal and diurnal growth here are not so good. Figures 27 and 28 give the curves of average hourly rate for day and for night growth in height. The night rate was found in both cases to be less than the daytime rate. For *P. nigra* the ratio of day to night rate is 1.6:1, and for *P. quadrangularis* 1.2:1, as far as the evidence goes. Both shoots of the Black bamboo follow the same general trend in their diurnal oscillations. More data are necessary to tell whether the same thing is true of the Square bamboo shoots. There is no doubt, however, that the consistent behavior of individual shoots of the same species with reference to day and night growth rates indicates the existence of definite specificity in growth processes.

For the study of seasonal and daily periodicity in rate of elongation, and their relations to environmental conditions, we need to consider the relative number of hours of daylight and darkness. Shanghai lies about 31° north latitude, and both growing seasons follow the equinoxes fairly closely. The spring seasons begin on April 21, and the fall seasons follow by three to four weeks the autumnal equinox. This would indicate an almost equatorial day for the growth of both species.

To what extent external factors actually do modify the daily rate of elongation can be judged by a careful comparison of the growth curves with corresponding curves representing environmental conditions. That oscillations do occur is shown by the minor undulations in figures 1 to 10. These are consider-

ably magnified in figures 12 to 16, and may be studied better in these cases. Slight irregularities are evident, but in general one is struck by the uniformity of the oscillations in the curves for the two species. Such synchronous oscillations suggest external controlling conditions. For example, in figure

TABLE 10

Comparison of tall shoots with short shoots with reference to rate of growth when one half of their final height

		PHYLLOSTACHYS NIGRA					
		1924		1925		1926	
		Tallest	Shortest	Tallest	Shortest	Tallest	Shortest
Shoot number		4	6	10	3	10	1
Height (final)		358	247	393	280	424	331
Increase on day when one-half height	Actual	28.4*	16.7	35.0	30.0*	42.5*	30.7
	Fraction of height[a]	.079	.068	.089	.107	.100	.093
Increase on day when one-half height averaged with increase on day before and day after	Actual	22.2	19.4	36.0	28.0	36.5	30.6
	Fraction of height[b]	.062	.079	.092	.100	.086	.092

[a] Average for tallest shoots, .089. Average for shortest shoots, .089

[b] Average for tallest shoots, .080. Average for shortest shoots, .090.

		PHYLLOSTACHYS QUADRANGULARIS			
		1925		1926	
		Tallest	Shortest	Tallest	Shortest
Shoot number		9	4	7	4
Height (final)		196.7	157.5	207.1	145.8
Increase on day when one-half height	Actual	10.5	11.4	11.9	11.2*
	Fraction of height[a]	.053	.072	.057	.077
Increase on day when one-half height averaged with increase on day befoe and day after	Actual	10.6	11.1	12.3	10.6
	Fraction of height[b]	.054	.071	.059	.073

[a] Average for tallest shoots, .055. Average for shortest shoots, .075.

[b] Average for tallest shoots, .057. Average for shortest shoots, .072.

* Maximum daily increment for that culm.

12 between May 12 and 13, 1924, the rate of growth of Black bamboo shoots is shown to have suddenly dropped. This drop is expressed in a marked depression in all the curves. A similar drop occurred between May 16 and 17, 1925 (fig. 13) and between May 6 and 7, 1926 (fig. 14). With the shoots of the Square bamboo the uniformity of such oscillations in rate is not so striking, partly because of the relatively smaller daily increment in this species and partly because of the fact that the shoots seem to be at more widely separated stages of their grand periods. Their growth rates are synchronous, but in varying degrees. For instance between October 20 and 21, 1925 (fig. 15), there is a noticeable depression in all the curves, the degree of which varies according to the stage of the grand period in which each shoot happened to be. In figure 16 there is a concurrent undulation, covering November 1, 2 and 3, whose synchronism is quite clear. Other instances of harmonious behavior than those mentioned are brought together in table 13. Such uniform modifications of behavior of a series of shoots without regard to species or stage of growth can not be ascribed to internal factors and must obviously be explained as reactions to external conditions. Reference to the curves for the mean daily temperature, relative humidity, and rainfall at the top of each figure brings out the fact that in all cases the depressions noted agree absolutely with corresponding dips in the curve of mean daily temperature. On the other hand, no matter what the extent of the reaction to these external factors, the general rise of the curve to and the descent from the maximum is not interfered with or materially altered but remains specific.

The logarithmic curves shown in figures 17 to 26 exhibit relative height increase, since logarithms of heights are plotted as ordinates against time in days as abscissae. In relation to the height of the shoot at any time, the increments day by day form a diminishing geometric series. The curves in general rise at a steep angle from the time axis and curve more sharply toward the horizontal as they sweep upward. This is the same as saying that the relative increment at first is large but decreases by geometric progesssion as the shoot elongates. Relative increase represents the amount of work done and is therefore a gauge of metabolic capacity. To illustrate the

point a simple example will suffice. We may consider the time that a shoot at any stage of its growth takes to double its height. Let any point on the curve (no. 4, fig. 17) be the initial point which can be read in terms of height as log x. The point on the curve, then, at which the shoot doubles its height will be log $2x$, or log $2+$ log x. From the initial point on the curve mentioned a perpendicular line may be erected equal in height to a distance of .301, or the logarithm of 2, on the scale of ordinates; from the upper end of this perpendicular line we may draw a horizontal line which intercepts the curve, thus determining a second point, corresponding to log $2x$. Perpendicular lines dropped from these two points to the time axis cut off a line whose length represents the time in days which the shoot takes to double its height. This unit is then an expression of the plant's growth rate specificity. If this process is repeated at regular intervals on the curve, the lengths of the time periods increase progressively as the upper end of the curve is approached, as shown, for example, by the intervals 2.4, 3.4, and 5.5 days in figure 17. In other words, the taller a shoot becomes, the longer is the time period required for it to double its height; this is true throughout the grand period of growth—when the actual increments (in centimeters per day) are rapidly increasing to a maximum as well as later when the actual increments are becoming progressively smaller. Furthermore, growth specificity is shown by this criterion if the graphs for *P. nigra* are compared with those for *P. quadrangularis*.

The conception of a determining chemical reaction as the underlying basis of rates of growth in length appears to find support in the results which I have obtained by a comparison of observed growth rates with corresponding rates computed from Robertson's formula for an autocatalyzed monomolecular reaction. The data for shoots no. 7 of 1925 *P. quadrangularis* and no. 10 of 1926 *P. nigra* were used in these computations, and the discussion is given in a later section.

SPECIFICITY OF THE GROWTH RATE

Internal factors

Bamboo is the fastest growing plant known. The greatest increase in height in twelve hours was recorded by Thomas

in 1921 (as reported by Galloway, 1925) who, when working with *Phyllostachys bambusoides* Sieb. & Zucc., observed a growth of 48.2 cm., and for a twenty-four hour period 91.4 cm. It was reported by Pfeffer (1903) that a bamboo in Kew Gardens was seen to grow 91 cm. in twenty-four hours. It is difficult to understand how such rapid growth is possible except on the basis of a large available food supply. When

TABLE 11

Day and night growth of Phyllostachys nigra, 1926[a]

DATE	SHOOT 1		SHOOT 5	
	Day	Night	Day	Night
April 21	.06	.02		
22	.02	.03		
23	.04	.04		
29	.21	.08	.17	.07
30	.36	.15	.16	.08
May 1	.55	.32	.28	.20
2	.74	.49	.36	.24
3	1.00	.70	.63	.44
4	1.15	.53	.74	.53
5	1.63	.97	1.09	.67
6	1.15	.64	.95	.42
7	1.95	.75	1.47	.62
8	2.27	1.19	1.26	.88
9	1.56	1.12	1.14	1.06
10	1.62	.62	1.63	.96
11	1.45	.79	2.21	1.35
12	.52	.52	.84	1.08
13	.42		1.81	

[a] The table contains the hourly day and night growth rates in cm. of two culms, involving 31 sets of observations. Of the 31 sets two show equal day and night rates and two show greater night growth. The ratio of average hourly day growth to average hourly night growth is 1.6 to 1.

the shoots become 30 to 60 cm. long, roots begin to grow down from just above the juncture of the sheathing bract and node at the base of the shoot. A. and C. Rivière (1878) figure a shoot of *Phyllostachys mitis* (p. 93) and one of *P. violascens* (p. 283), the former with three tiers of roots beginning to push downward before the shoot has attained more than 30 cm. in length. Though the evidence is not entirely clear, the proba-

bility seems to be that the period of growth rate acceleration begins when the first roots from the base of the shoot become fully established. The food supply apparently consists of carbohydrates, in the production of which at least the young shoot has had little or no part, and water with food salts in solution in part at least absorbed from the soil by the new culm roots. Just what portion of the available supply of carbohydrates in the beginning is relayed through the rhizome from other parts of the plant and how much is drawn from the original supply stored as starch in the bud is not easily determinable, but it seems unlikely that it should all come from an initial quantity of materials deposited in the bud. I have planted out cuttings of rhizomes with a piece of old culm attached, and also cuttings with entire culms intact, and in both cases the buds and shoots of the first year or two were undersized. Superficially the growth habit of bamboo shoots resembles that of asparagus, but actually it is different and might be said to occupy a place intermediate between asparagus and barley. The growth of barley has been carefully analyzed by Gregory (1926); but the problem in this case is much complicated by the presence of both leaves and a root system, and these must be taken into consideration in the study of the grand period.

At first the bud is a small, hard, fusiform structure closely appressed to the side of a node of the rhizome. When the growing season approaches, the bud begins to swell. As soon as it becomes as thick as the mature culm will eventually be, no further increase in diameter takes place and elongation commences. The bud, which has been a solid mass of overlapping sheathing bracts, now starts to lengthen and the leaf bases commence to draw away from one another, showing the internodes (plate 10). The progress of elongation of the shoot as a whole and of each internode is always from the base upward. When active elongation is fully under way, a great many internodes are elongating at the same time, but each one is in a different stage of its special grand period. The basal internode is the first to attain its full length, then the next higher, and so on. The sheathing leaves have a phyllotaxy of one-half and a divergence of 180°, and in the bud they are concentrically arranged. They envelop the entire circumference of the internodes, overlapping a third again the entire distance

around the periphery of the internode. The inner surface of the sheathing leaves is very smooth, and when elongation takes place they slide on each other like the parts of a telescope. As each internode nears its mature length, the region of elongation becomes confined more and more to the basal end. The sheathing leaves on account of their stiff leathery texture, besides protecting the intercalary zones from injury, provide mechanical support and stiffening. Lock (1904) measured the extent of the growing region in shoots of *Dendrocalamus giganteus* and found that when the shoot was 7.3 to 9.5 meters tall, the length of the growing region averaged 4.9 meters; that above 11 meters the length of the growing region extended to 6 meters; and that toward the final height its length fell off, till by the time the topmost internodes were elongating the growing region had become confined to them. In every growing internode cell division, cell stretching, and cell differentiation are going on concurrently, all taking place in turn in each internode, in seeming independence of every other internode.

TABLE 12

Day and night growth of Phyllostachys quadrangularis, 1926[a]

SHOOT NUMBER	NOV. 9		NOV. 10		NOV. 11		NOV. 12		NOV. 13	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
1	.36	.26	.20	.15	.15	.26	.21	.26	.12	.07
2	.26	.23	.13	.17	.21	.18	.18	.14	.10	.04
3	.25	.15	.14	.08	.03	.16	.12	.10	.05	.03
4	.16	.06	.06	.06	.12	.006	.06	.04	.01	.006
5	.56	.33	.32	.20	.31	.25	.18	.28	.06	.006
6	.67	.60	.50	.43	.40	.43	.41	.51	.13	.11
7	.38	.25	.31	.15	.20	.18	.18	.19	.02	.01
8	.31	.13	.24	.05	.21	.08	.11	.07	.03	.01
9	.63	.38	.25	.17	.30	.23	.25	.31	.00	.04
10	.75	.53	.50	.25	.41	.31	.42	.40	.16	.06
11	.51	.50	.53	.37	.81	.34	.40	.47	.23	.13
12	.70	.56	.52	.38	.47	.51	.51	.58	.21	.09

[a] The table contains the hourly day and night growth rates in cm. of twelve culms over a period of five days, involving 60 sets of observations. Of the 60 sets one shows equal day and night rates and 13 show greater night growth. The ratio of average hourly day growth to average hourly night growth is 1.2 to 1.

Growth rates in different species. Among the shoots of *P. nigra*, number 3 of 1926 showed the most rapid rate of

growth. Its maximum gain in twenty-four hours was 49.5 cm., or a little less than 12 per cent of its whole height. Of the shoots of *P. quadrangularis*, number 7 of 1926 showed the greatest growth in twenty-four hours; this was 16.3 cm., or about 8 per cent only of its total height. The Rivières (1878) in 1872 observed the growth of *P. nigra* in Algiers where the shoots spring up at the same time of the year that they do in Shangai, China. The culms in Algiers reached a little greater height, though just how much is difficult to say, for the daily increment of only one culm is published, and the initial measurement of this is lacking. The daily gains add up to 546.9 cm., but this can not be the total height, for that would mean that the first day's increase from the zero point was 14.0 cm., which is quite unlikely. This particular culm must have been a little over 6 meters in height. However, the daily gain seems to have been consistently high, like that of the Shanghai shoots, and the length of the grand period fairly short. Actual measurements for twenty-five days are given. I plotted the curve of daily increment and it shows at once that there were very wide oscillations in rates from day to day. For instance, on April 25 the day's increase amounted to 19.9 cm., on the next 40.0 cm., and on the following day 24.3 cm. The Rivières seem to have made records of climatic conditions, but only a few are published. The greatest increase in twenty-four hours made by the Black bamboo of Algiers was 40.0 cm., a little less than that made by my fastest growing shoot. The first day's recorded gain for the Shanghai shoot (no. 3, 1926) was 2.9 cm., starting from an initial height of 8.7 cm. In nine days the shoot was over the meter mark, in three more days it was two meters, in three more days it was over three meters and had begun to slow down, and by the end of twenty-two days the shoot had reached a height of 414.5 cm.

It is quite apparent that there are both fast growing and slow growing species of bamboos, but from the data available at present it is impossible to formulate specific growth averages with any degree of accuracy. Much depends of course on when the initial measurements are made. There is as yet no standard practice in this respect. Among the fast growing forms *Dendrocalamus giganteus*, *Phyllostachys bambusoides*, *P. mitis*, and *P. nigra* seem to stand out. Though a study of published growth

measurements of *Dendrocalamus* shows a maximum of only 57 cm. in a day (Kraus, 1895), an isolated report (Pfeffer, 1903, p. 15) gives a maximum of 91 cm. in twenty-four hours. The

TABLE 13

Summary of growth data in relation to atmospheric conditions of temperature and moisture[a]

DATE	YEAR	RAINFALL	RELATIVE HUMIDITY	TEMPERATURE	GROWTH RATE
		mm.		°C	
May 11	1924	None	Constant 87.2	Rise 19.12	Rise
" 12	"	Rain 10.6	Constant 87 2	Drop 14.22	Drop
" 14	"	" 27.5	Rise 95.6	Low 15.51	Check
" 15	"	None	Drop 82.0	Rise 18.32	Peak
" 18	"	Little 1.0	Rise 79.8	Fall 16.64	Drop
" 12	1925	Rain 89.9	Peak 97.0	Rise 17.23	Rise
" 16	"	" 2.7	Rise 89.1	Low 16.65	Drop
" 19	"	None	Drop 69.7	Peak 21.01	High
" 20	"	"	Low 66.2	Fall 19.78	Drop
" 5	1926	Rain 4.7	High 87.2	High 21.29	Rise
" 8	"	None	Drop 58.0	" 19.84	High
" 11	"	"	Low 75.3	Peak 21.61	Peak
" 12	"	Rain 15.0	Peak 92.5	Drop 16.94	Fall
" 13	"	None	Fall 79.1	Rise 18.83	Rise
Oct. 8	1925	None	High 78.3	Peak 19.90	Rise
" 18	"	"	Constant 75.9	Peak 17.55	Rise
" 27	"	"	Fall 74.0	Rise 18.06	Peak
" 27	1926	"	Peak 91.8	Fall 15.87	Fall
" 30	"	"	Drop 58.9	Drop 7.53	Drop
" 31	"	"	Rise 70.4	Low 8.36	Low
Nov. 2	"	"	Constant 76.4	Rise 13.15	Rise
" 9	"	Rain 1.5	Rise 89.5	High 16.72	High
" 10	"	None	Constant 88.0	Fall 15.82	Fall
" 12	"	Rain 1.7	Constant 88.2	Rise 19.67	High
" 13	"	None	High 90.1	Fall 15.05	Drop
" 14	"	Rain 1.3	Drop 75.4	Drop 9.57	Drop

[a] May is growing season for *P. nigra;* October and November, for *P. quadrangularis.*

average growth rate per day for the period of observation is given by Kraus as 19 to 22.9 cm. per day. *P. bambusoides*, in growing to a height of 12.2 meters in five to six weeks, is said

to elongate at a rate of 30.6 cm. a day. This seems high, but I have no other data with which to compare it. Among the slow-growers are *P. quadrangularis* and *Bambusa vulgaris*. *B. vulgaris* in the Philippines takes four to five months to attain 15 or 16 meters, growing at a daily average rate of 12 to 13 cm. In Algiers the culm measured was a little over 7 meters high, to which height it grew in 31 days, growing 14 cm. a day on the average. Despite differences in height and in location, the average rate is close enough to indicate that growth rate is more or less specific.

With reference to the specific growth rates of *P. nigra* and *P. quadrangularis* the evidence is more adequate, but these are a spring and a fall species, respectively. Table 6 presents an analysis of tables 1–5 with relation to rate of growth of representative shoots from the 29 culms of *P. nigra* measured over three years' time and from the 23 shoots of *P. quadrangularis* measured during two years. Among the shoots of *P. nigra*, there are considerable differences in the size attained, in the number of days of the grand period, and in the maximum rate reached, but there is a consistent contrast throughout with the corresponding data for *P. quadrangularis*. The individual differences between shoots of the same kind may be due to the youth or age of the rhizome from which they spring, the time of growth with reference to the specific optimum season, or to various unknown differences, but these individual variations appear to fluctuate about a rather definite mean value that is characteristic of the species in question, and the mean value for one species seems likely to be very different from that for another species. Table 7 contains the average growth rates for the series of years of observation on the basis of the representative shoots mentioned above. Thus, *P. nigra* in 1924 grew at an average rate of 13 cm. per day, in 1925 at 17.8 cm., and in 1926 at 18.4 cm. The average number of days required to complete the growth period is 25, 19, and 22, respectively. The average rate for the three years is 16.4 cm. a day, and the corresponding average time is 22 days, the height of the shoot at the beginning of measurements being about 7.5 cm. *P. quadrangularis*, on the other hand, averaged 4.5 cm. per day in 1925 and 5.9 cm. per day in 1926, the time of growth being 37 and 29 days, respectively. The average rate

for both years is 5.2 cm. per day, and the average number of days 33, from an average initial height of 15 to 20 cm. The spring conditions in which *P. nigra* grows are as follows: an ascending temperature fluctuating at first around 12.5–16.0°C., then finally between 20 and 22°C.; an average daily rainfall of 3.9 mm.; and a relative humidity averaging approximately 83 per cent. The fall conditions in which *P. quadrangularis* grows are: an average mean daily temperature of 14.5°C., a rainfall averaging only 1.2 mm. daily, and an average humidity of 76 per cent. Taking the evidence as it stands, specificity of growth rate is clearly indicated.

A. and C. Rivière (1878) state that a shoot grows fastest when it becomes as tall as that point on a mature culm where the longest internodes are located. This is equivalent to saying that growth rate and ultimate length of internode are directly correlated. To test this point, it was necessary to measure older culms with reference to the length of their internodes and to compare them with shoots that had reached approximately a similar height. One typical culm of both species was measured in this way. The measurements are given in table 8, together with daily measurements of the growth of shoot 4, 1925, Black bamboo and shoot 9, 1925, Square bamboo.

All shoots of *P. nigra* that approximated 324.0 cm. in total height were selected from tables 1, 2 and 3, and those of *P. quadrangularis* close to 200.0 cm. from tables 4 and 5. This is a very indirect method and further investigations are much needed. The data (tables 8, 9) suggest no correlation between the length of the longest internode and the maximum rate of growth, and none between the height of a shoot while growing most rapidly and the height of that region in the culm where the internodes are the longest. The longest internode of the culm of Black bamboo is 20.4 cm., and it is 105.1 cm. above the base of the culm. The shoots which grew ultimately to a height nearest that of the culm in question, however, had a maximum rate of 37.9 cm. on the day when the shoot was 221.4 cm. high. The longest internode of the culm of Square bamboo is 9.9 cm. at a height at 55.4 cm. The nearest corresponding shoot, on the other hand, had its maximum rate of 13.7 cm. at 77.8 cm. above the ground, showing again no agreement between maximum length of internode and

maximum growth rate, or between position of longest internode and height of shoot at fastest period of elongation.

The Rivières also conclude that the maximum growth per day is found to occur toward the middle of the height attained by the culm. My observations agree with this conclusion. In their measurements of *Phyllostachys mitis*, for instance, the day on which the culm reached just half its full height was the day before it had made its maximum growth. The culm attained its full height, 751.7 cm., on June 16. It was half that height, or 375.8 cm., on May 24. It was on May 25 that the maximum gain was made. Table 10 gives the results of an investigation of the relative rates for tall shoots and short shoots. The interesting thing here is that in four of the ten shoots investigated (marked '*') the day on which the culm came to its halfway point was the day of maximum gain. Shoots nos. 6 and 1, Black bamboo, had their maxima on the day after the halfway point was reached, while no. 10, 1925, had its maximum on the day before. Nos. 9 and 7, Square bamboo shoots, were half of their completed height on the day after they had had their maximal gains; shoot no. 4 of 1925 was half its final height several days before the maximum. The evidence suggests a uniform tendency of bamboos to have their greatest gain on the day they are half of their ultimate height, though this point need not necessarily be the middle day of the grand period. It is of particular interest that the mathematical equation applied most successfully to growth assumes this same relation.

With regard to the relative growth rates of tall shoots and short shoots, there also is uniformity of behavior in different species. Usually the shorter shoots grow at a slower rate than the tall ones, but when considered in percentage of the total height, the relative rate of the shorter shoots is greater. Table 10 gives the data for the tall and short shoots of each species for every year. The comparison is made with reference to the rate of growth when at half the mature heights of the culms. By averaging this rate with that for the day before and the day after, an approximate rate for the period was obtained and in every case except no. 9, 1925, Square bamboo, the average rate of the tall shoots is greater than that of the short shoots. When compared with reference to

rate of growth in percentage of the total height, however, the short shoots of both species average higher than the tall shoots.

The tall shoots of *P. nigra* together averaged 31.5 cm. per day at their halfway points, the short shoots 26.0 cm., or 83 per cent of the rate of the tall shoots. The tall shoots of *P. quadrangularis* together averaged 11.4 cm. per day at the same point, the short ones, 10.8 cm., or 95 per cent of the rate of the tall shoots. This difference of relation between the rates of growth of tall and short shoots of *P. nigra* and those of *P. quadrangularis* gives a suggestion of specificity in the range of growth rate at the time when the shoots are one-half their mature height.

Daily periodicity. Probably nowhere is the interrelation of the external and internal factors of growth so well demonstrated as in its daily periodicity. Sachs (1882) in 1872 was the first to study daily periodicity under controlled conditions as to light and other factors. He concluded that under constant conditions of temperature, moisture, and darkness irregular variations of growth were still observable, a fact which seemed to indicate that the causes of daily periodicity are independent of external changes and lie in the plant itself.

The recent work of Garner and Allard (1920) on photoperiodic responses of plants has helped to clarify our ideas with regard to the nature of both seasonal and daily periodicity. Many species of plants have a specific optimum length of day for vegetative growth and flowering, respectively. Any alteration or change in this factor throws the organism, so to speak, out of stride in the cyclic alternation of growth and reproduction. In the light of the work of these investigators, the seasonal range of day length becomes an important factor in the adaptation of the organism to its environment.

Bamboos have a very definite daily periodicity in their growth. In the spring of 1926 I measured two shoots of *P. nigra* twice daily for most of their grand period, and plotted their curves in terms of hourly rate (fig. 27). In the autumn I did the same thing with twelve shoots of *P. quadrangularis*, but only over a period of five days. The periodicity curves of these shoots in terms of hourly rate are shown in figure 28. The measurements are tabulated in tables 11 and 12. Both of these

species appear to have a definite daily periodicity and both of them grow faster in the day than in the night. The day to night ratio for *P. nigra* is 1.6 to 1 and for *P. quadrangularis* 1.2 to 1. This difference, though not by any means sufficient to be conclusive, is suggestive of possible specificity in this particular.

The daily periodicity curves of shoots nos. 1 and 5 of *P. nigra*, though characteristically alike, present individual differences as well as synchronic variations. I took no hourly readings of temperature or relative humidity and therefore have no evidence as to how fluctuations in diurnal and nocturnal rates of growth are related to these factors.

On May 5, 6, and 7 (fig. 27) there is a close parallelism in a growth oscillation, which undoubtedly may be referred to external conditions. On the night of November 10 (fig. 28) there is a noticeable depression in all the growth curves, due perhaps to a drop in the temperature. Lock measured two shoots of *Dendrocalamus* hourly from 3:30 p.m. on June 22 to 11:30 a.m. on June 23 and from 5:30 a.m. on June 29 to 5:30 p.m. He concludes that the hourly oscillations which he observed are due to moisture.

Probably the most outstanding case of marked external influence of daily growth rate is that of *Cestrum nocturnum* studied by Brown and Trelease (1918). This plant elongated in the night but in the day it actually shrunk when the sun shone. Lock postulated conditions of atmospheric moisture as determining the daily periodicity of his shoots. The Messrs. Rivière assert that the autumn-growing species with which they worked, *Bambusa macroculmis*, *B. vulgaris*, and *B. vulgaris vittata*, grew more rapidly at night, and that the spring-growing forms, *Phyllostachys viridi-glaucescens*, *P. nigra*, and *P. aurea*, with the exception of *P. mitis*, grew faster during the day. The failure of the growth of *P. mitis* to accord with that of the others growing at the same time and under the same conditions is a marked case of specificity in this particular.

It is probable that when photoperiodism is investigated with reference to the growth of bamboo shoots, more light on the question of periodicity of growth will be had. We should not neglect the possibility that inherent response to an optimum day length might prove to be the underlying factor in periodical oscillations of growth rates. If this were true, the degree of

response would be a reflection of the specific character of the plant, and bamboo shoots, no matter where found, provided they were of the same species and were growing in localities having approximately equal day lengths, would exhibit similar ratios of day and night growth. Some evidence which would seem to support this hypothesis may be derived from the literature. Kraus (1895), Lock (1904), and Osmaston (1918) all found that *Dendrocalamus* grew more rapidly at night than in the day. The ratios of night growth to day growth were found to be 1.8 to 1, 2.8 to 1, and 2 to 1, respectively. This means that the growth of *Dendrocalamus giganteus* in Java (about 9°S.), Ceylon (about 9°N.), and India (Calcutta, about 22°N.) growing respectively from November to January, from June to August, and from August to November, under tropical conditions and tropical day length, presumably twelve hours day and twelve hours night, exhibits a characteristic and specific daily periodicity. *P. nigra* has been measured both in Algiers (37°N.) and in Shanghai (31°N.), China. A. and C. Rivière found in Algiers that this species grew faster during the day than during the night, and that the ratio of day growth to night growth was 1.7 to 1. I find that the Shanghai shoots of *P. nigra* also grew faster by day than by night (table 11) and that the ratio of day growth to night growth is 1.6 to 1, which is a close agreement.

Seasonal periodicity. Is an autumn-growing bamboo like *Phyllostachys quadrangularis* always an autumn-growing bamboo, no matter where it grows, or does it sometimes become spring-growing? *P. quadrangularis* has not been studied on this point anywhere else than in Shanghai, so that the question cannot be answered for this species. *P. nigra*, however, both in Algiers and in Shanghai, grows in the months of April and May. Freeman-Mitford (1896) also reports from England its growth in April and May. *Phyllostachys mitis* in Algiers grows from May 25 to July 8, in Japan (Tokio, 36°N.) from April 24 beyond May (Shibata, 1900), and in England in late summer. Shoots of the English plants were seen only in the first and third summer on one plant, and on another in the second summer but none in the third. *P. viridi-glaucescens* seems to have the same growth season in England as in Algiers (April–May). *P. aurea* in England begins to come in April, but its growth period is

from May through June in Algiers. The available data suggest that some species of bamboo tend to start their growth at the same season in the year wherever they may be found or are transported. Nevertheless their growth periods may be moved from spring slightly on toward summer or pushed back or set forward a little from the autumn according to prevalent external conditions.

Effect of external factors

The external factors that most concern the growth of bamboo are those of soil and atmosphere.

Soil. The soil on which both of my patches of bamboo grow on the St. John's Campus is alluvial silt and is therefore very fertile and favorable for a wide range of plant types. The Square bamboo flourishes on a cleared spot somewhat shut in and overhung by the high branches of tall trees. The ground is covered for part of the year with fallen leaves. The Black bamboo, though sheltered on the north by a building and bordered on the south with a row of medium-sized trees, is more in the open. I have not analyzed the soils on which they grow chemically, nor have I made any records of soil temperature and of moisture content. The latter can be partially gauged by the fact that silt has a very low porosity, and by considering this in connection with the amount of rainfall as shown in my records.

Light. Both the immediate and the ultimate effects upon growth of changes in light intensity have been much studied in recent years. Lock (1903) notes that culms do not appear to be phototropic, and that it is hard to see how light can greatly affect the growing region through the thick opaque armour of leaf sheaths. By shading a small shoot with a cylindrical cover of tin he tested the question further. He tried the experiment on two species, with a control in each case of the same height as those under observation. Both capped culms grew at the same rate as the controls. No direct effect of light seemed to be involved.

When the shoot has nearly ceased to elongate and the last sheathing leaves are falling off, I observed a loss of height after a sunny day. This is undoubtedly due to an excessive loss of water through transpiration from the surface of the

young culm. This lessens turgescence to such an extent that the shrinkage resulting more than offsets the amount of increase in length characteristic of that period. A. and C. Rivière, in attempting to measure intercalary growth, removed the sheathing leaves from growing internodes, and found that the internodes abruptly stopped growing. This may be a traumatic effect, an effect of increased transpiration, or a direct effect of illumination. Apparently the experiment shows not only a checking of growth, but also a hastening of the internal processes of differentiation and specialization which bring about hardening of the tissues.

So far I have made no experiments on the effect of light on growth rates, nor have I carried on any studies of the specific effects of length of day (photoperiodism). In view of the very marked effects obtained by Garner and Allard (1920) on the relation of photoperiodism to blooming and growth, it would be of great interest to test bamboo with its very marked cyclic habits of blooming as to possible photoperiodic effects on both growth and blooming.

Lock studied especially the changes in rate of growth as related to variations in moisture conditions. Hourly measurements taken in conjunction with readings of the psychrometer revealed a marked parallelism between the two curves, 'whilst the curve of temperature had an almost exactly opposite character.' He concludes that changes of moisture are the chief cause of the observed oscillations in the growth rate of *Dendrocalamus* shoots. But after reconsidering Shibata's data, which showed great variations in mean daily temperature with corresponding variations in rate of growth, and also changes of atmospheric moisture which seemed to have evoked little response, he was moved to modify his conclusions to the effect that possibly the apparent results upon growth of changes in moisture conditions were due, in part at least, to the very constant mean temperature which prevailed at Peradeniya during the period of his observations. In other words, given a constant mean temperature, the rate of growth may respond to changes in atmospheric moisture, but with fluctuating mean temperatures, the rate of growth parallels more closely the rise and fall of the mean daily temperature. The same reason may possibly explain why Kraus in Java was impressed with Sachs'

conception of 'sudden spontaneous variations' in growth rate as more significant than external conditions. Though he gave no daily records, it seems that the conditions of both moisture and temperature at Buitenzorg were very constant, in which case, of course, individual peculiarities and physiological differences in the various shoots were bound to be more noticeable.

Moisture. Moisture and temperature are apparently the two most important external factors influencing the growth of bamboos. In figures 12 to 16 the curves for fifty-two culms, accompanied by the curves for the variations in mean daily temperature, relative humidity, and rainfall, are shown. A high degree of correlation, especially between rate of growth and temperature, is obvious.

In examining my results I find no indication of agreement between changes in rate of growth and either relative humidity or rainfall. For instance, on May 16, 1924, the relative humidity was decreasing, the temperature was rising, and there was no rain, and yet the growth rate in three cases actually rose, in five cases remained high though following maxima, and in one case (no. 2) went down lower than the day following. On May 13, 1925, the relative humidity was going down, the temperature was up, there was light rain following a heavy rain the day before, but without exception the growth rate went up. The moisture content of the air on May 16 of the same year was high, there was rain, but the temperature was down. The growth rate was also down. In 1926 the relative humidity went up on May 9, the temperature took a small drop, there was also rain, yet the growth rate went down. So much for *P. nigra*. In the fall I found the same results in my study of the growth rate of *P. quadrangularis*. On October 18, 1925, the mean daily temperature went up, the relative humidity had been constant around 75 per cent for nearly a week, no rain fell for nearly a month, but the growth rate went up. With rain on November 3, 1926, a high percentage of air moisture, and a drop in temperature, the growth rate dropped. So from my evidence the growth rate of the two Shanghai species seems not to be greatly affected by changes in moisture conditions.

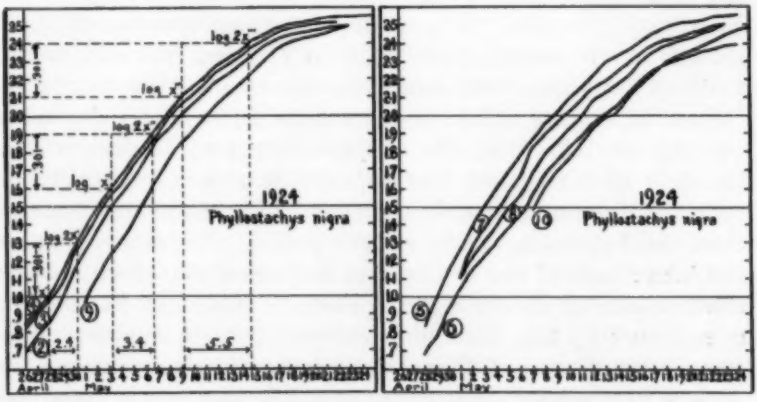
It may be expected, however, that a very high evaporating power of the air or a very low water supplying power of the

soil may have a marked influence on the growth and distribution of bamboos. Though temperature sets a general limit on their northward advance, atmospheric moisture may determine their distribution within wide areas below their northern limit. In making a survey of the bamboo industry in China some years ago for the Chinese Government Bureau of Economic Information (1925), I found that bamboos were more abundant on hills and plains in the southern coastal provinces and in the regions near large bodies of water, where they would be likely to be bathed frequently with fogs and mists.

With the exception of five days it rained every day during the time Kraus (1895) was measuring his giant bamboos in Java, and it required 58 to 60 days for them to complete their growth at an average rate of 19 to 22.9 cm. per day, while Lock (1904) found the same species attained its height in Ceylon in 55 days at an average rate of 28.6 cm. per day with varying rainfall. The effect of moisture may be seen in the behavoir of Brown and Fischer's (1918) shoots in the Philippines. Most rapid growth was found to occur nearer the end than the beginning of the growth period. Growth is slow in the latter part of the dry season, but upon the advent of the rainy season all shoots begin to elongate more rapidly, though even then they take from four to five months to complete their growth; while one of the same species, *Bambusa vulgaris*, in Algiers (A. and C. Rivière, 1878) 22° farther north, took less than two months. On the other hand, Osmaston (1918) at Dehra Dun found new culms of *Dendrocalamus* commenced to elongate in the middle of the rainy season and completed growth two months after it. He asserts that the maximum growth rate develops when the relative seasonal humidity is highest.

Temperature. Every plant may be considered to have an optimum temperature for growth, though this optimum may be influenced somewhat by any one of a number of non-temperature conditions. With seedlings, Sachs (1860) showed that *Triticum vulgare* grows most rapidly at 28.7°C., *Hordeum vulgare* at the same temperature, *Cucurbita Pepo* at 33.7°C., *Phaseolus multiflorus* and *Zea Mays* at the same temperature. The results of Köppen, De Vries, and others agree fairly well with those of Sachs. Above or below optimum temperatures

the rate of growth diminishes and ceases when they become sufficiently extreme. Most studies have been made with constantly maintained temperatures; little attention has been given to fluctuating temperatures. Detailed studies have shown that the optimum temperature depends upon the kind of plant and upon its phase of development, upon the duration of exposure, and upon various other conditions, such as light, moisture, etc. It has been ascertained, says Sachs, that when long periods of time such as entire days are compared, the effects of all other conditions of growth are outweighed by the effects of the variations of temperature, so that in general



Figs.17, 18. Logarithmic growth curves of *P. nigra* 1924 shoots 2–10. (Ordinates, logarithms of heights.)

the rapidity of growth increases and decreases with temperature changes. This statement of course applies only when the non-temperature conditions are adequate for rapid growth. The data in table 13 suggest that for *P. nigra* and *P. quadrangularis*, growing under the conditions prevailing at Shanghai, temperature is the dominant factor in changing the growth rate of aerial shoots. This is perhaps the more obvious since both species are near their northern limit at Shanghai.

There can be no question for these bamboos in the given locality that the variations in growth rate follow closely the rise and fall of temperature. Whenever the temperature curve rises (figs. 12–16) the growth curves of daily rate, with very few exceptions, rise also. For instance, on May 20, 1925, the

temperature dropped and so did the growth rate. The same thing happened on October 30, 1926, and on November 14, 1926. But the situation becomes complicated when we notice that the relative humidity fell also. Was not the fall in growth rate due to the fall in atmospheric moisture, or the rise in growth rate on November 9, 1926, due to the rise in the moisture content of the air? If one examines the twenty-two other cases cited, one will see that, with two other exceptions, the temperature and relative humidity curves move in opposite directions. Where the humidity is marked 'constant,' movements up and down in temperature and growth rate have occurred irrespective of its stationary condition for the few days in question. Rain, as pointed out, seems also to have had no effect. On the ten dates in the table when it rained, six were accompanied by an actual lowering of the growth rate. One of these was merely a check at a time when the rate of growth was on the rise. The other four dates showed rises. If, however, the temperature in relation to growth rate is examined on these same ten occasions, it will be seen that in every one of the cases there was absolute agreement. From the evidence there is no alternative but to conclude that for *P. nigra* and for *P. quadrangularis* under the given conditions temperature is the most potent single factor in governing the rate of growth.

A striking case of correlation between rate of growth and temperature variation is seen in the following data extracted from one of Shibata's tables (1900) on the daily growth of *Phyllostachys mitis* in Japan:

Extract from Shibata's table

DATE	DAILY INCREMENT FOR SIX SHOOTS, CM.						MEAN TEMPERATURE °C.	MEAN REL. HUMIDITY %	WEATHER
MAY	I	II	III	IV	V	VI			
1	20.1	22.6	28.7	22.0	39.8	43.5	16.7	73.0	Windy
2	31.0	34.4	41.8	33.1	53.8	61.7	18.4	66.0	Quiet
3	38.0	41.1	47.5	38.2	66.0	66.9	17.6	80.0	Rain
4	23.2	28.3	30.2	27.6	39.8	40.3	13.8	91.4	Windy

The facts reported here for bamboo are in agreement with the results of Barber (1919) from his studies of Indian sugar canes. Barber found that declines of warmth and moisture

check the growth of the canes. They grow most rapidly in the north of India during the months of heavy rainfall and great heat. Gilbert (1926) working with varieties of soy beans, *Cosmos*, *Salvia*, cotton, and buckwheat, was able to isolate the effects of external factors experimentally, by growing his seedlings under controlled and contrasted conditions. Under relatively constant conditions of day length, with temperature and humidity as variables, he found the modification of response obtained very great. The cotton and his four varieties of soy beans showed very favorable response to warm temperature (25–28°C.) and low humidity (50 per cent), but in the cool house with the temperature varying between 17.2° and 21.7° and the relative humidity at about 85 per cent, the growth rate was much lower; they grew 7.6 to 12.7 cm. less in five weeks. This parallels my results with bamboo shoots, except that for the latter the conditions were not controlled.

It is very difficult to trace the effect of temperature on growth rates of bamboos in the data from other writers, because of the variation in other varying conditions, and especially the incompleteness of the records. Kraus (1895) worked under a practically constant mean temperature which regularly varied each day between 23° and 32°C. In Peradeniya Lock (1904) found the extreme limits of the temperature range from June to November to be 17° and 26.6°C. but the mean daily temperature he found varied from 23.3 to 26.1°C. The day to day variations were so slight that in the face of much greater changes in conditions of moisture, direct correlations between temperature and growth rate can not be traced. A. and C. Rivière (1878) published very few data on temperature and none on relative humidity. A great many temperature readings were taken daily, on one occasion from October 26 to 31, 1876, but no corresponding measurements of growth. I worked out the mean temperatures for the days in question and applied them in the table to the daily growth measurements of *Bambusa vulgaris*, which grows at that time, but could find no correlation. The mean temperature during those seven days was practically constant, the range of variation being 16.1–17.7°C. Brown and Fischer (1918) say nothing about either temperature or relative humidity in connection with their Philippine bamboos.

Wind. Wind probably affects the growth rate of bamboos

only indirectly. Wind, together with temperature and relative humidity, of course determines the evaporating power of the air, and the latter, acting with light, strongly influences transpiration, especially of older culms. Lock (1904) alone has considered the effect of wind. He remarked that high winds were rare and that they were usually accompanied by heavy rain. The inference seems to be that since it rained, adverse effects on the growth rate by the wind were thereby effectually neutralized. He did not make any attempt to trace in detail such relations as might exist. In figures 1 to 10, I note in the daily columns the presence or absence of high wind. On May 17, 1924, it was windy, the temperature went down, and all but two of the curves dipped (figure 12). The situation was a little different, however, on May 12, 1925, when there was a heavy rainfall. The temperature was up and the growth rate rose also (figure 13). On October 28 of the same year there was a high wind, a depression of the temperature, and also an accompanying fall in growth rate (figure 15). In 1926 no high winds were noted in the spring season, but they did occur in the fall on October 9 and 19. In the former case the temperature was dropping and the growth rates of the shoots (Square bamboo) responded variously; four down, two up, and four checked. In the latter case the wind was accompanied by a check and drop in temperature and a very decided drop in the growth rates of all shoots (figure 16).

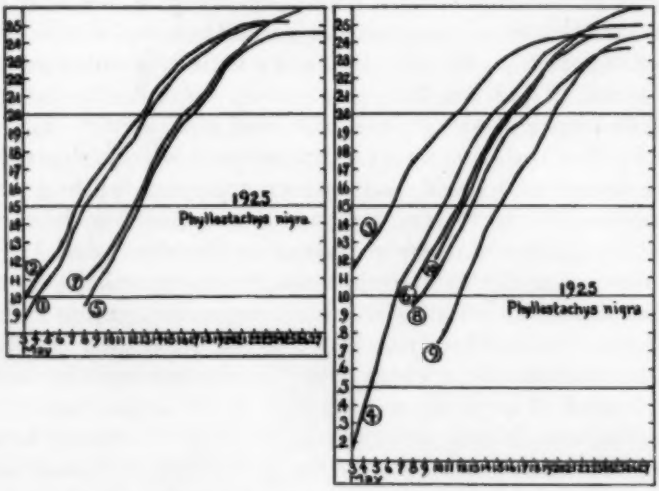
Cultivation. It was previously noted that the average height of the new culms of *P. nigra* for the years 1924, 1925, and 1926, respectively, was greater each year. This may be explained by one or both of two things, failure to cut them back to the same extent as had been done previously, and prevention of crowding by other shrubs and trees. All shoots that heretofore came up in the grass, I had cut back to preserve the lawn, but after commencing the years of measurement, I let them grow. In addition to this I cut out young saplings of *Ailanthus*, *Brousonettia*, and other fast growing trees that were wont to spring up and crowd out the bamboos. I noticed that subsequently the shoots in general seemed to be larger and the culms to be taller.

THE AUTOCATALYTIC CONSTANT AS AN INDEX OF GROWTH RATE SPECIFICITY IN BAMBOOS

The definiteness and constancy of the grand curve of growth suggests that it should be easy to find a mathematical expression

for the growth processes of which it is a picture. If such an expression should really prove to be valid, it could be used as a basis for physiological comparisons, and from it could be calculated indices of physiological activities. As I have just shown, there seems to be a normal velocity of physiological activity connected with growth which is specific for different plants. An index of such activity for any plant therefore should be a very definite expression of its specificity.

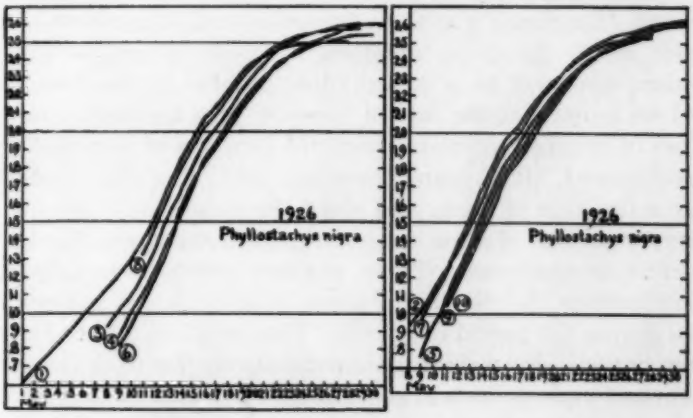
In 1906 Noll employed what he called the 'Substanzquotient' in growth. This is obtained by dividing a number



Figs. 19, 20. Logarithmic growth curves of *P. nigra* 1925 shoots 1–10. (Ordinates, logarithms of heights.)

representing the dry weight of a plant at the end of any period of its growth by a number representing its dry weight at the beginning of that period. This quotient was applied by Gressler and others to the growth of *Helianthus* and *Cannabis*, but the calculations were based on data secured after relatively long periods of time, sometimes several weeks, so that the use of this method seems to imply that growth is a discontinuous process, by which at regular intervals growth increments are added in geometric progression. Blackman (1919) has emphasized the fact that growth is a continuous process and that increment is being added continuously, and he has applied

the compound interest law to the growth of plants. The rate of change of some quantity is proportional to the quantity itself, as he states the proposition. He reasoned that the leaf area increases as the plant grows. This increases the capacity for assimilation, which brings about more rapid growth. A still greater leaf area results and therefore a still greater production of assimilating material. If the rate of assimilation per unit area of leaf surface and the rate of respiration are constant, the size of the leaf system bears a constant relation



Figs. 21, 22. Logarithmic growth curves of *P. nigra* 1926 shoots 1–10. (Ordinates, logarithms of heights.)

to the dry weight of the whole plant, and the rate of production of new material as measured by dry weight is proportional to the size of the plant. Therefore the plant in its increase of dry weight will follow the compound interest law. The form of the equation which is used in the application of this idea is as follows:

$$W_1 = W_0 e^{rt}$$

in which W_1 is final weight; W_0, initial weight; t, the time interval; e, the base of the natural logarithms; and r, the rate of 'interest' at which the plant is continuously adding to its 'capital.' In its logarithmic form for the solution of r the equation becomes:

$$r = \frac{\log_e W_1 - \log_e W_0}{t}$$

It is obvious from the formula that final weight depends on initial weight, rate of growth, and time. Blackman considered '*r*' as an important 'constant' or index and, because of its economic value and physiological significance, he called it the efficiency index. When the rate of growth was observed to fall after the first few weeks of growth, he attributed it to a fall in efficiency which was correlated with the mechanical relations involved in growth.

Briggs, Kidd, and West (1920) in their quantitative analysis of plant growth brought out the fact that if the rate of growth (Blackman's *r*) is to be considered a constant in the strict sense, the curve obtained by plotting rate of growth against time will be a straight line parallel to the time axis. But we know that the rate of 'interest' goes through a definite series of changes correlated with the progress of morphological development. It appears, therefore, that '*r*' is not a constant but a function of time, and since the values of '*r*' found for varying periods of time are not the same, they can hardly be used in comparisons. These workers proposed to take into consideration the varying relations of assimilation and respiration during the period of growth. They employed data derived from periodic dry-weight measurements representing the whole plant and various parts at short intervals of time, corresponding leaf area measurements, as well as data with regard to light, temperature, and water supply. A large enough number of plants of pure line material was used to compensate for individual variation. From the primary data thus obtained, the relative growth rate or the rate of increase of dry weight per unit of material per unit of time, the leaf area ratio, or the ratio of leaf area to dry weight, the unit leaf rate or the rate of increase in dry weight per unit of leaf area per unit of time, and the relative leaf growth rate or the amount by which a unit of leaf dry weight increases per unit of time may be calculated. By a careful consideration of these values in comparison with each other and with records of environmental factors, they assert that one might ultimately evaluate plant growth constants. The whole purpose is to account for all irregularities in the grand period curve by correlating rate of growth with the influence of internal and external factors, a difficult task.

From an entirely different point of view, that in which growth rate is conceived as conditioned by the velocity of chemical reactions taking place in the growing organism, a closer approach to a significant constant seems to have been

TABLE 14

Values used for plotting straight line (figs. 29, 30) from which logarithm of specific growth constant (K) is derived

NO. 7, P. QUADRANGULARIS, 1925				NO 10, P. NIGRA, 1926			
$\log(\log \frac{x}{196-x})$		$\log(t-25.2)$		$\log(\log \frac{x}{424-x})$		$\log(t-14.8)$	
$t<t_1$	$t>t_1$	$t<t_1$	$t>t_1$	$t<t_1$	$t>t_1$	$t<t_1$	$t>t_1$
.413	.413	1.38	1.27	.365	.418	1.13	.96
.350	.359	1.36	1.25	.305	.387	1.10	.91
.296	.292	1.34	1.22	.248	.220	1.07	.85
.262	.262	1.32	1.19	.195	.060	1.03	.79
.233	.233	1.30	1.17	.155	−.087	.99	.71
.220	.209	1.28	1.13	.110	−.190	.94	.62
.179	.198	1.26	1.10	.049	−.309	.89	.50
.136	.173	1.23	1.07	−.011	−.466	.83	.34
.071	.127	1.20	1.03	−.101	−.762	.76	.07
.049	.096	1.18	.99	−.160	−1.482	.68	−.69
.021	.045	1.15	.94	−.256		.57	
−.002	−.012	1.12	.89	−.399		.44	
−.012	−.086	1.08	.83	−.546		.25	
−.037	−.145	1.04	.76	−.861		−.09	
−.073	−.255	1.00	.68				
−.115	−.387	.96	.57				
−.149	−.546	.91	.44				
−.198	−.729	.85	.25				
−.251	−1.066	.79	−.09				
−.336		.71					
−.458		.62					
−.591		.50					
−.717		.34					
−.944		.07					
−1.639		−.69					

made. Robertson (1908), in discussing the normal rate of growth of an individual and its biochemical significance, was the first to apply the autocatalytic equation to growth processes. As explained by him, the processes of growth, like those occurring in the hydrolysis of cane sugar, may be regarded as repre-

senting an autocatalyzed monomolecular reaction. This implies that growth is a self-accelerated reaction; the presence of newly synthesized protoplasm and its elaborations is considered to be the favoring condition for its further production in greater and greater amounts until the reaction is gradually brought to an end, either by exhaustion or transformation of the substrate, or by an accumulation of the products of the reaction, this accumulation resulting in the acceleration of the reverse reaction to the point where its velocity equals that of the forward reaction. It is assumed that an autocatalyzer is produced, an x-substance, which is connected with the orderly changes in growth rate. Temporary modifications of the growth rate by external factors as shown by minor irregularities in the grand curve do not seriously affect the characteristic course of the autocatalytic reaction or the efficiency of the autocatalyst. Many studies have shown that the mathematical equation which represents an autocatalytic chemical reaction also represents with a high degree of accuracy the growth of many different kinds of plants and animals.

Brody and Ragsdale (1921) found that growth constants which were derived from the formula for autocatalysis were representative of the rates of different growth cycles in the life of the dairy cow, and Robertson (1923) applied the equation to Donaldson's data on the growth of white rats. In plants Reed and Holland (1919) have used it in their studies on the growth of *Helianthus*. Gaines and Nevens (1925) in crop studies, Gregory (1926) on the growth of barley, and others have also used it with impressive effect. Van de Sande-Bakhuyzen and Alsberg (1927), however, hold that a number of the assumptions on which this method of treatment is based are as yet unproven, and they raise the question whether the very simple methods of analyzing growth rates proposed by a number of investigators may not be misleading.

Waldron (1921) in studying the rate of culm formation in *Bromus inermis* applied Blackman's compound interest law of plant growth, but no evidence could be found that it had any real organic significance. Because of the misleading implications as to the 'r' in Blackman's equation, as previously noted, I have not attempted to apply it. Nor have I further applied the methods suggested by Briggs, Kidd, and West, inasmuch as

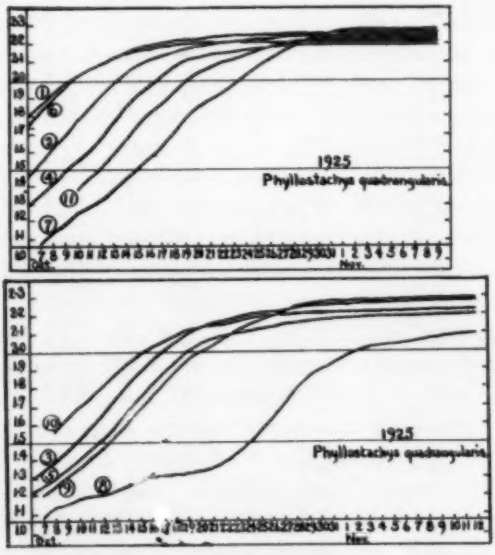
TABLE 15

Values of x,t, and of computed t when K = .095 for shoot no. 7, 1925, of P. quadrangularis and when K = .157 for shoot no. 10, 1926, of P. nigra.

P. QUADRANGULARIS			P. NIGRA		
t	*x*	*t* when *K* = .095	*t*	*x*	*t* when *K* = .157
1	.5	−2.1	1	2.0	−.007
2	1.1	1.4	2	4.0	1.9
3	2.0	4.2	3	7.0[a]	3.5
4	2.8	5.5	4	11.0	4.7
5	3.7	7.0	5	14.9	5.6
6	4.7	8.2	6	20.4	6.5
7	6.0	9.2	7	29.3	7.6
8	8.0[a]	10.7	8	40.6	8.5
9	12.0	12.6	9	58.9	9.7
10	13.7	13.2	10	71.6	10.4
11	15.8	14.0	11	92.5	11.2
12	18.0	14.7	12	121.0	12.3
13	18.8	14.9	13	144.5	13.0
14	21.0	15.5	14	178.5	13.9
15	24.3	16.2	15	221.0	15.0
16	28.0	17.0	16	254.2	15.8
17	32.0	17.7	17	291.2	16.9
18	37.0	18.5	18	320.6	17.9
19	42.2	19.2	19	346.0	18.9
20	50.2	20.2	20	368.2	20.0
21	60.6	21.4	21	396.5	22.1
22	69.8	22.4	22	415.1	25.4
23	76.7	23.1	23	422.5	30.3
24	85.1	23.9	24	424.0	....
25	95.5	24.9			
26	108.0	26.0			
27	119.0	27.0			
28	129.2	28.1			
29	141.3	29.5			
30	153.4	31.0			
31	164.5	32.7			
32	170.2	33.7			
33	177.1	35.4			
34	182.0	36.8			
35	185.7	38.3			
36	187.6	39.3			
37	189.7	40.8			
38	191.0	41.8			
39	191.5	42.2			
40	192.3	43.2			
41	193.2	44.4			
42	193.9	45.8			
43	195.0	49.3			
44	195.5	52.2			
45	196.0	....			

[a] From this point upwards, values extrapolated, not actual—*i.e.*, from 1 to 8 and from 1 to 3, nclusive.

no leaves appear on the culm until long after elongation has ceased. The ephemeral sheathing leaves, which die as soon as the internodes that they embrace have ceased to grow, can hardly be considered as contributing to the essential economy of the plant, so that no leaf-areas of the culm in question can be included in the calculations as relating to the grand period of its growth. As intimated elsewhere, for lack of more exact determinations, the bamboo shoot for the present must be considered as a growing part of the plant which elongates on

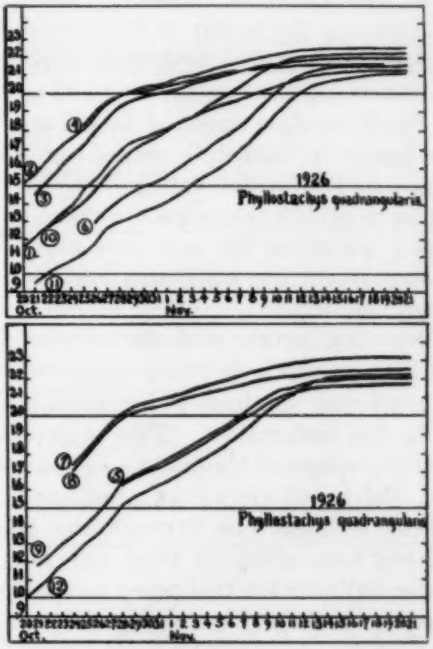


Figs. 23, 24. Logarithmic growth curves of *P. quadrangularis* 1925 shoots 1–11. (Ordinates, logarithms of heights.)

the basis of stored food in the original bud. This is augmented and later more or less replaced by the available supply of materials from the rhizome and the older culms and by an increasing flow of materials from its own growing basal roots as the shoot pushes upward. Since the culm during the grand period of its axis develops no leaf-area, the logical conclusion is that its elongation is at least largely, and from the standpoint of carbohydrate supply almost wholly, due to internal rather than external factors, the latter being concerned chiefly

with the *rate* of elongation. The question of the root relations of the young culm needs further study.

In order to test the usefulness of Robertson's formula as a basis for computing growth constants for bamboo, calculations were carried through with one shoot from each of the two species. Shoot 7 of the 1925 Square bamboos and shoot 10 of



Figs. 25, 26. Logarithmic growth curves of *P. quadrangularis* 1926 shoots 1–12. (Ordinates, logarithms of heights.)

the 1926 Black bamboos were selected as exhibiting representative curves. The form of the equation applied by Robertson is employed:

$$\log \frac{x}{A-x} = K(t-t_1),$$

in which A is total height; x, the height at any time, t; and t_1, the time at which the shoot is one-half its full height. K is the specific growth constant.

The measurements of the two shoots from tables 4 and 3, respectively, were plotted separately against time as in figures 31 and 32, and the time units converted into numbers of days instead of being left as days of the month. The curves were then arbitrarily extended to the base line and the initial measurements extrapolated. Since the calculations are based on the time at which a shoot is one-half its full height, it was necessary to estimate the extent of this period. By inspection of the curve representing observed growth values, it was noted that for the Square bamboo shoot, A is 196 cm. and t_1 is 25.2, and for the Black bamboo shoot, A is 424 cm. and t_1 is 14.8. The values of x and t for each daily record were then substituted in the equation. The noted values of t_1 and A, of course, remained the same in each operation. In this manner the growth constant K was computed for each time unit. The values for K, which showed slight but consistent variation at the extremities, were then averaged.

Before proceeding further with the computed curves, let us consider another approach to these calculations. As a check to the mathematical method of computation a graphical solution for K was undertaken. This might have been done simply by plotting values of $\log [x/(A-x)]$ as ordinates and the corresponding values of $(t-t_1)$ as abscissae. After having drawn the 'best' straight line through the points, the value of K could have been obtained from any point on this line by dividing the ordinate for this point by the abscissa. However, it seemed desirable to determine at the same time whether the modified formula suggested by Reed (1921) would be more accurate for representing the growth of these bamboos. Accordingly, curves were constructed the ordinates of which were the calculated values of the expression $\log \{\log [x/(A-x)]\}$ and the abscissae those of the expression $\log (t-t_1)_c$. This treatment assumes a more general form of the growth equation to be $\log [x/(A-x)] = K(t-t_1)^c$, in which the exponent c may or may not be unity. The logarithmic form of this equation is $\log \{\log [x/(A-x)]\} = \log K + c \log (t-t_1)$. When $t < t_1$ the values of $(t-t_1)$ are negative in sign. When $t > t_1$ the values of $(t-t_1)$ become positive. The signs, however, do not affect the logarithms; they simply show that there are two sets of determinations. These are tabulated in separate columns in table 14. When both

sets of points have been determined, they should approximate a straight line (figs. 29 and 30). The point at which the 'best' line intercepts the y-axis is the approximate logarithm of K. And the corresponding value of c is the slope of the line; to obtain this the intercept on the y-axis is divided by that on the x-axis. The curve for the Square bamboo shoot cuts the y-axis at about 1.01. Log K is -1.01 and K is .097. For the

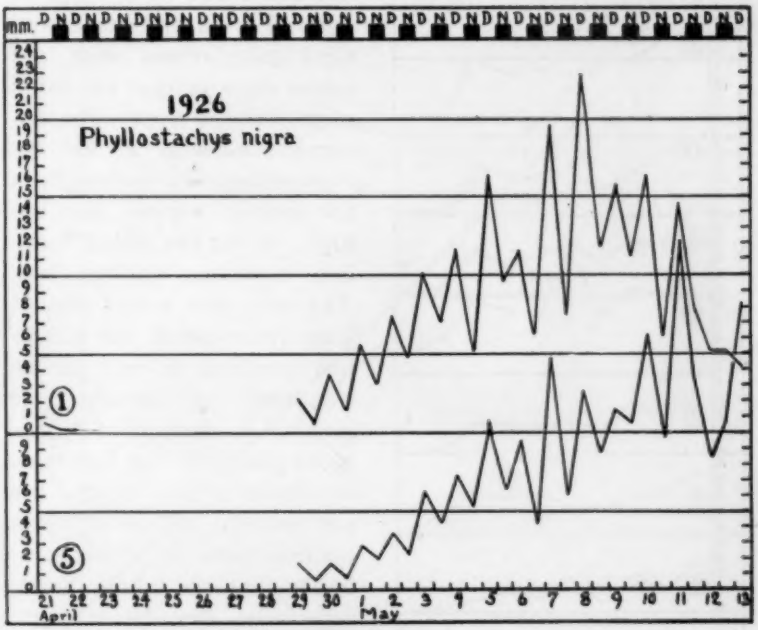


Fig. 27. The growth curves of *P. nigra* 1926 shoots 1 and 5 for fifteen days, showing daily periodicity of growth in length.

Black bamboo shoot the interception is approximately at .83. Log K is $-.83$ and K is .151. The difference between unity and the value of c is so small in each case that it may be regarded as negligible. Thus, for the growth of these bamboos, the simpler formula may be considered to be as accurate as the more general equation suggested by Reed (1921).

The values of K derived from figures 29 and 30 and the values of K calculated from Robertson's formula were then substituted in the original formula with the original values of

x and the equation was solved for t. The resulting curves when compared with those representing the actual measurements did not show sufficiently close approximation, which was evidence that better values of K might be chosen. Both of the curves derived from the mathematical calculations were too steep, showing that the value of K was too high. The observed value of K for the Square bamboo, derived from the graph, proved also too high. K for the Black bamboo, however, was too low. The fact that errors should arise from use of the graphical method is not to be wondered at since it is largely a matter of judgment just how the line is to be drawn if the points are not exactly aligned. Upon consideration it seems probable that the whole curve, especially the latter part, after it has flattened out, is not truly representative of an autocatalytic reaction, and that the last measurements should not be taken into consideration. After several trials, I found that by dropping off the last nine measurements of *P. quadrangularis* and the last two of *P. nigra*, an average value for K resulted from which curves of

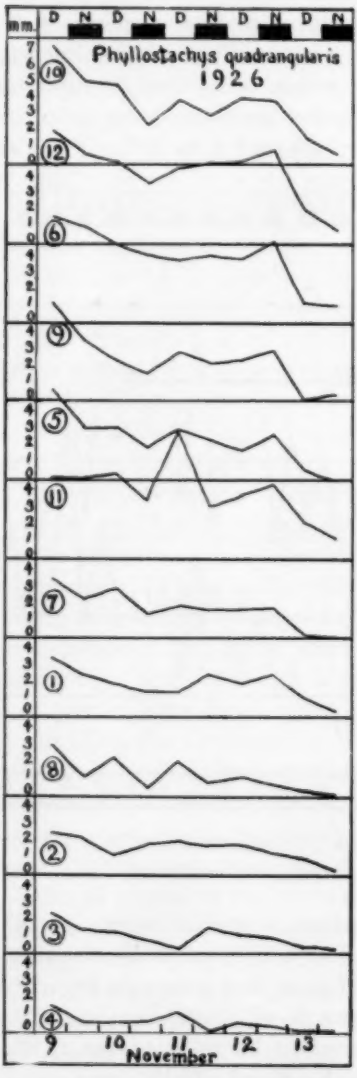


Fig. 28. The growth curve curves of *P. quadrangularis* 1926 shoots 1–12 for five days, showing daily periodicity of growth in length.

almost exact approximation could be plotted. The K of the former was calculated to be .095 and K of the latter, .157. The computed values of t appear in table 15. It will be seen that with this treatment of the data there is very close agreement in each case between the calculated grand period curve and

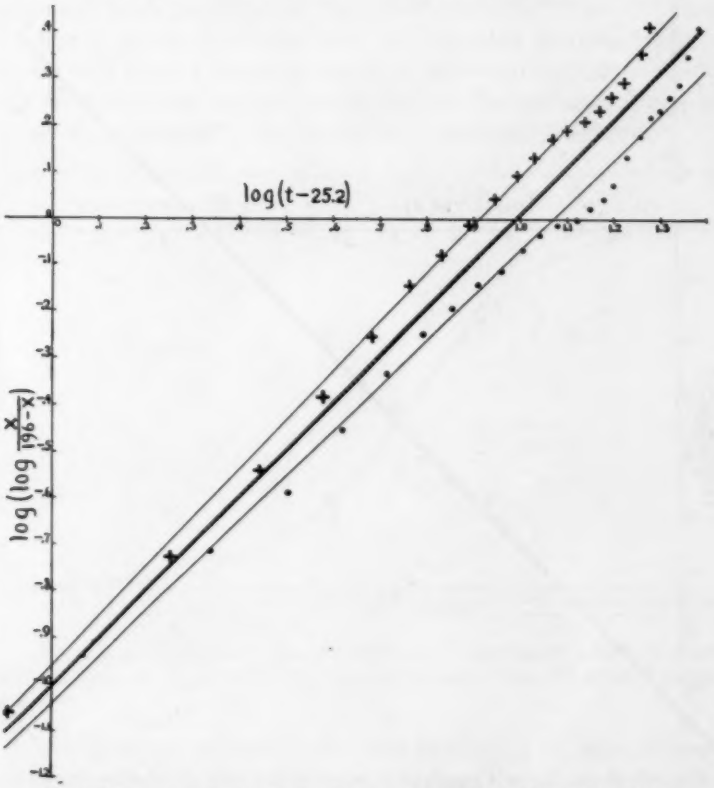


Fig. 29. Autocatalytic graph of *P. quadrangularis* 1925 shoot 7. Dots, values when $t<t_1$; crosses, when $t>t_1$.

the corresponding curve plotted from actual observations. To have been exact the intercept of the straight line on the y-axis in figure 33 should have been at -1.02 and in figure 34 at $-.81$.

In order to gauge in another way the degree of approximation between the grand period curves and their computed equivalents, I plotted the observed times against the calcula-

ted t. The result, if a straight line, would mean exact agreement. Figure 34 better than figure 33 expresses the linear relation expected. The deviations in the latter figure would probably become smaller if a sufficiently large number of

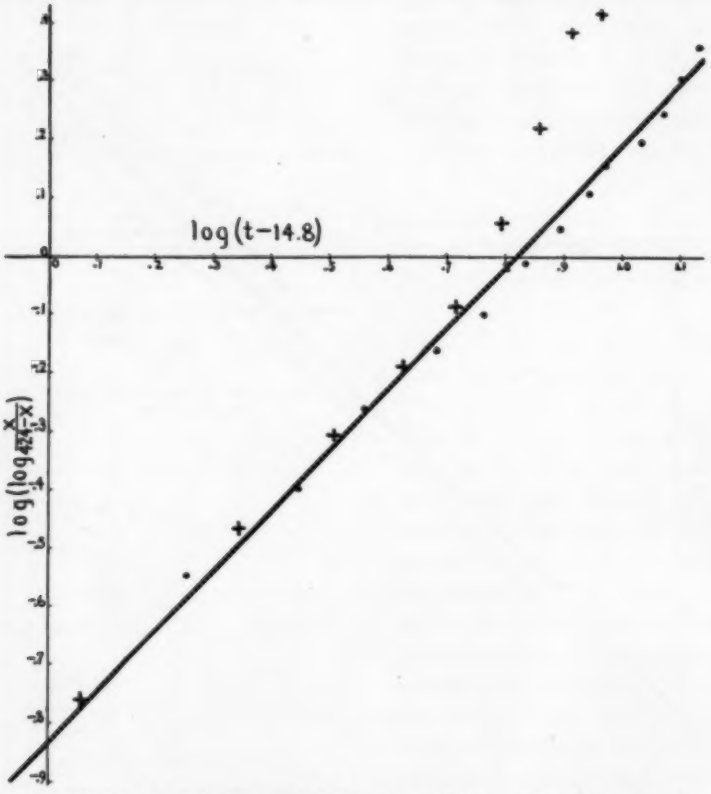


Fig. 30. Autocatalytic graph of *P. nigra* 1926 shoot 10. Dots, values when $t<t_1$; crosses when $t>t_1$.

shoots was measured and the data were subjected to a similar treatment.

The graphs of figures 31 and 32 show that the equation that represents an autocatalyzed monomolecular reaction also represents with a high degree of accuracy the growth of these bamboos. The usefulness of Robertson's equation in expressing the growth of bamboo is thus established.

The results of the present work indicate definitely that the rate and duration of growth processes in the bamboo shoot, as reflected in the difference of the growth constants, is a function of specificity in the plant itself. Though the K herewith computed for these two shoots can hardly be expected to represent with precision all the other shoots of their respective species, it seems probable that the average growth constant, K, derived from a larger number of shoots from various places and from different seasons, if carried out for both species, would show approximately the same characteristic difference.

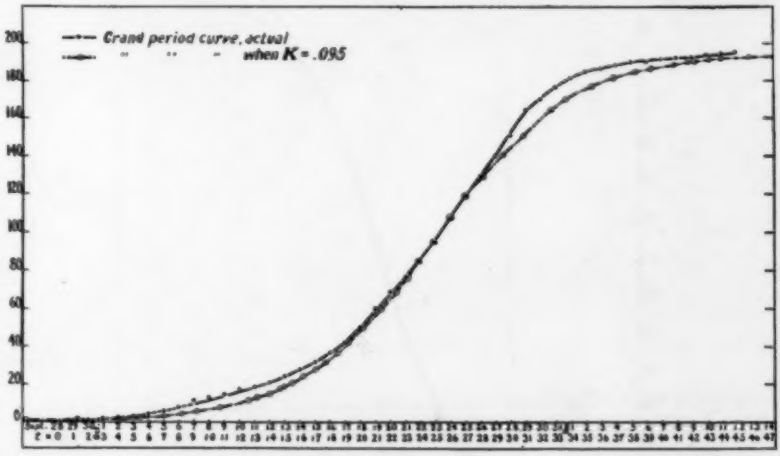


Fig. 31. Comparison of growth curve of *P. quadrangularis* 1925 shoot 7 with curve computed from Robertson's formula. Specific growth constant $K = .095$.

No attempt will be made here to discuss the question as to whether growth really involves an autocatalyzed monomolecular reaction. The quantitative data obtained in the present study confirm the observations of other workers that both growth and the autocatalytic reaction may be represented by the same mathematical expression. This, of course, does not prove that the two processes are qualitatively alike. A single mathematical equation may represent a number of processes that are quite different in their nature. Nevertheless, many striking analogies between the two processes have been pointed out by Robertson and others, and the conception of growth as an

autocatalyzed monomolecular reaction is an extremely suggestive working hypothesis.

SUMMARY

1. The daily measurements of 29 shoots of *Phyllostachys nigra* (Black bamboo), a spring-growing species, for a period of three years, and of 23 shoots of *Phyllostachys quadrangularis* (Square bamboo), a fall-growing species for two years, at St.

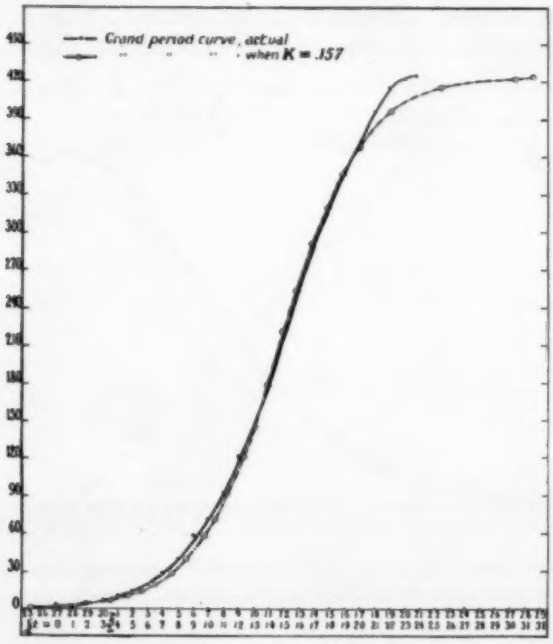


Fig. 32. Comparison of the growth curve of *P. nigra* 1926 shoot 10 with curve computed from Robertson's formula. Specific growth constant $K = .157$.

John's University, Shanghai, China, show consistent differences in the amount of daily increment. The average growth rate of *P. nigra* in 1924 was 13.0 cm. per day, in 1925, 17.8 cm., and in 1926, 18.4 cm. The average time required to complete their growth was 25, 19, and 22 days, respectively. For *P. quadrangularis* the average rate of growth was 4.5 cm. in 1925, 5.9 cm. in 1926, and the time required was 37 and 29 days, respectively.

2. The grand period curves (representing height plotted against time) for all shoots are S-shaped, smooth, and regular, but those of *P. nigra* show characteristic differences from those of *P. quadrangularis*. The former rise higher and more steeply from the base line (time axis) and turn more sharply at the ends than those of the latter. Despite differences among individuals of a species, the curves have a form that is characteristic of the species.

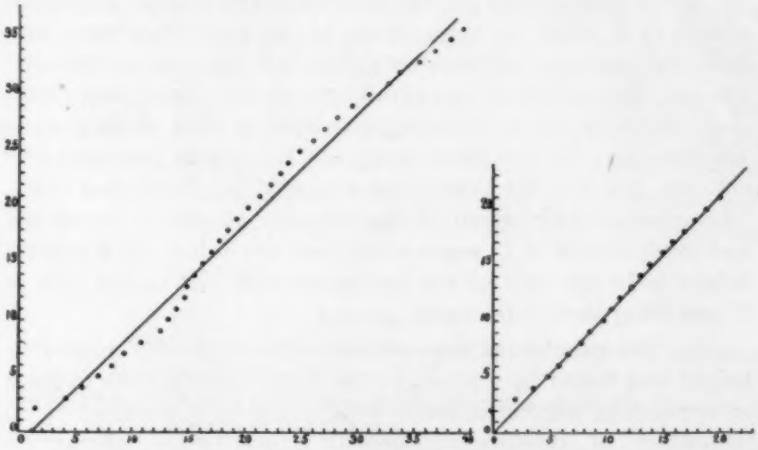


Fig. 33 (left). Graph showing straight-line relation between computed time (abscissae) and actual time (ordinates) of *P. quadrangularis* 1925 shoot 7, the culm height being the same for each.

Fig. 34 (right). Graph showing straight-line relation between computed time (abscissae) and actual time (ordinates) of *P. nigra* 1926 shoot 10, the culm height being the same for each.

3. A comparison of a representative grand period curve for Black bamboo (no. 10, 1926) with a typical curve for Square bamboo (no. 7, 1925), each based on height measurements in percentage of total height, shows that while the latter took ten days to elongate 16 per cent (22%−6%), the former took only 4.37 days; while it took ten days for the latter to reach 72.5 per cent, it required only 6.63 days for the former; and while ten more days were required for the Square bamboo shoot to reach 98 per cent, the Black bamboo shoot made it in 4.50 days.

4. The maximum gain was shown to occur approximately on the day when the shoot is one-half of its mature height. This is characteristic of bamboos generally, and is a fundamental assumption involved in the formula for a monomolecular autocatalyzed reaction, which Robertson and others have employed to represent the growth of many kinds of living organisms. The largest individual gain for a single day was 49.5 cm. for *P. nigra* and 16.3 cm. for *P. quadrangularis*.

5. A comparison of the growth rates of tall and short shoots of *P. nigra* for three years, at the time when they were half their mature height, shows that tall shoots averaged 31.5 cm. per day and short ones 26.0 cm. per day (or 83 per cent). Tall shoots of *P. quadrangularis* compared with short ones in the same way for two years show that the former averaged 11.4 cm. per day and the latter 10.8 cm. per day (or 95 per cent). The characteristic mean of variation in growth rates of tall and short shoots of *P. nigra* when they are half of their mature height is 18 per cent of the maximum rate and in the case of *P. quadrangularis* 6 per cent.

6. The number of days which a shoot takes to double its height was found by a study of the logarithmic curves to form an expanding geometric series which may be considered as an indication of diminishing growth capacity as elongation proceeds. The rate of expansion is shown by the slope of the curves and is more rapid in shoots of *P. nigra* than in those of *P. quadrangularis*.

7. Measurements taken twice daily show that shoots of both species grew faster in the day than in the night. The largest increase in an hour was 22.7 mm. by a shoot of *P. nigra*. The largest hour's elongation made by shoots of *P. quadrangularis* was 7.5 mm. The ratio of day-to-night growth was 1.6:1 and 1.2:1, respectively.

8. The records of climatic conditions under which *P. nigra*, the spring form, and *P. quadrangularis*, the fall form, grew reveal the following differences: mean daily temperature averages in the spring, about 18°C.; the relative humidity, 83 per cent; and the rainfall, 3.9 mm. The mean daily temperature in the fall averages about 14.5°C.; the relative humidity, 76 per cent; and the rainfall, 1.2 mm.

9. The curves of daily growth show marked synchronous rises and falls which were referred to external conditions. By the very close agreement between fluctuations in temperature and the changes in rate of growth, in spite of varying conditions of moisture, it is demonstrated that temperature is the most potent external factor affecting the growth rate of these bamboo shoots.

10. The application of Robertson's formula for a monomolecular autocatalyzed reaction to a representative shoot of each species shows that with a value of .157 for the specific growth constant, K, of shoot no. 10, 1926, *P. nigra*, and of .095 for that of shoot 7, 1925, *P. quadrangularis*, close agreement was obtained in each case between the curve computed from the formula and those that are based on actual daily measurement.

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Explanation of plate 10

Shoots of *Phyllostachys nigra* Munro in various stages of growth.

TABLE 1

Measurements, in centimeters, of shoots of Phyllostachys nigra from April 26 to May 26, 1924

DATE	1		2		3		4		5		6	
	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN
Apr 26	8.6		5.0		6.7		7.0		.....		.....	
27	10.5	1.9	6.1	1.1	8.3	1.6	8.6	1.6	.....	....	.....	....
28	12.0	1.5	7.1	1.0	9.7	1.4	10.1	1.5	6.9	....	4.8	....
29	15.9	3.9	9.7	2.6	11.8	2.1	13.5	3.4	10.0	3.1	6.0	1.2
30	20.5	4.6	14.0	4.3	17.4	5.6	18.6	5.1	14.3	4.3	8.6	2.6
May 1	23.1	2.6	18.2	4.2	22.2	4.8	24.2	5.6	18.9	4.6	11.0	2.4
2	26.9	3.7	23.5	5.3	29.0	6.8	31.5	7.3	25.0	6.1	14.0	3.0
3	31.5	4.6	30.9	7.4	36.3	7.3	39.8	8.3	32.0	7.0	17.0	3.0
4	35.0	5.5	37.7	6.8	43.5	7.2	47.2	7.4	39.9	7.9	20.0	3.0
5	36.5	1.5	45.5	7.8	53.3	9.5	58.0	10.8	50.0	10.1	24.3	4.3
6	37.6	1.1	57.3	11.8	63.7	10.7	69.1	11.1	61.0	11.0	28.4	4.1
7	38.4	0.8	74.6	17.3	78.7	15.0	86.0	16.9	75.0	14.0	37.8	9.4
8	....	...	85.7	11.1	98.0	19.3	106.5	20.5	93.0	18.0	48.0	11.2
9	....	...	101.3	15.6	115.0	17.0	121.7	15.2	104.0	11.0	58.1	10.1
10	....	...	116.7	15.4	131.1	16.1	138.1	16.4	128.0	24.0	66.7	8.6
11	....	...	133.1	16.4	151.2	20.1	158.2	20.1	144.1	16.1	76.9	10.2
12	....	...	157.2	24.1	176.6	25.4	186.6	28.4	172.5	28.4	92.1	15.2
13	....	...	171.7	14.5	193.1	16.5	204.8	18.2	188.3	15.8	99.0	6.9
14	....	...	194.8	23.1	218.1	25.0	228.7	23.9	214.9	26.6	114.9	15.9
15	....	...	213.4	18.6	242.7	24.6	252.2	23.5	232.4	17.5	131.6	16.7
16	....	...	248.8	27.4	269.7	27.0	278.7	26.5	263.5	31.1	157.2	25.6
17	....	...	259.7	16.9	291.1	21.4	304.0	25.3	289.2	25.7	175.3	18.1
18	....	...	279.0	19.3	303.4	12.3	320.5	16.5	303.5	14.3	192.5	17.2
19	....	...	287.7	8.7	314.8	11.4	329.5	9.0	317.0	13.5	203.0	10.5
20	....	...	299.7	12.0	324.6	9.8	341.0	11.5	328.8	11.8	215.0	12.0
21	....	...	308.0	8.3	333.0	8.4	350.0	9.0	338.0	9.2	226.2	11.2
22	....	...	316.0	8.0	337.7*	4.7	355.5	5.5	349.0	11.0	238.7	12.5
23	....	...	319.6	3.6	.....	....	356.9	1.4	354.4	5.4	246.0	7.3
24	....	...	.....	....	.....	....	357.5	0.6	357.0	2.6	247.6	1.6
25	....	...	.....	....	.....	....	358.0*	0.5	....	....	.....	....

* injured

TABLE 1—(cont.)

Measurements, in centimeters, of shoots of Phyllostachys nigra from April 26 to May 26, 1924

DATE	7		8		9		10		MEAN DAILY TEMPERATURE	RELATIVE HUMIDITY	DAILY RAINFALL
	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN			
Apr 27	.....		.....		.....		.....		13.0	56.0	....
27	.....	....	.....	....	.....	....	.....	....	13.8	68.0	....
28	.....	....	.....	....	.....	....	.....	....	16.0	76.5	....
29	.....	....	.....	....	.....	....	.....	....	20.7	82.5	16.7
30	.....	....	.....	....	.....	....	.....	....	16.2	83.5	1.4
May 1	12.7	....	12.9	....	9.5	....	.....	....	16.3	84.7	1.9
2	19.0	6.3	16.5	3.6	13.0	3.5	.....	....	14.7	97.5	14.8
3	24.2	5.2	21.0	4.5	17.0	4.0	.....	....	14.3	96.6	3.7
4	30.1	5.9	25.0	4.0	20.7	3.7	.....	....	15.8	94.4	6.2
5	39.0	8.9	31.0	6.0	26.7	6.4	.....	....	14.8	91.8	1.2
6	47.7	8.7	37.6	6.6	35.4	8.7	.....	....	15.7	95.5	2.0
7	68.0	20.3	48.1	10.5	44.8	9.4	30.5	....	19.3	97.0	22.3
8	78.5	10.5	62.0	13.9	58.4	13.6	42.2	11.7	18.3	90.4	3.3
9	90.0	11.5	72.1	10.1	71.0	12.6	50.6	8.4	15.9	73.5	0.1
10	105.3	15.3	85.7	13.6	82.3	11.3	59.4	8.8	15.2	87.8	3.6
11	121.3	16.0	99.2	13.5	97.8	15.5	71.6	12.2	19.1	87.2	....
12	141.8	20.5	120.4	21.2	117.1	19.3	87.3	15.7	14.2	87.2	10.6
13	154.1	12.3	130.0	9.6	129.8	12.7	96.3	9.0	15.5	92.9	6.9
14	175.0	20.9	150.2	20.2	154.0	24.2	102.6	6.3	15.5	95.6	27.5
15	195.8	20.8	168.0	17.3	174.8	20.8	130.0	27.4	18.3	82.0	....
16	220.2	24.4	199.8	31.8	205.1	30.3	149.0	19.0	20.1	75.6	....
17	246.2	26.0	227.2	27.4	237.3	32.2	172.8	23.8	18.0	73.9	2.9
18	264.4	18.2	247.2	20.0	251.3	14.0	196.3	23.5	16.6	79.8	1.0
19	275.0	10.6	262.0	14.8	274.4	23.1	209.8	13.5	16.4	94.8	12.3
20	287.7	12.7	274.0	12.0	279.0	4.6	228.5	18.7	17.1	82.5	0.5
21	300.0	12.3	286.6	12.6	293.0	14.0	247.0	18.5	19.5	78.3	..
22	310.2	10.2	299.8	13.2	309.0	16.0	266.4	19.4	21.0	82.0	....
23	316.5	6.3	319.8*	20.0	321.5*	12.5	284.0	17.6	20.1	91.6	21.0
24	.....	....	.....	....	.....	....	295.3	11.3	21.5	71.3	....
25	.....	....	.....	....	.....	....	303.0	7.7	23.0	66.7	....

TABLE 2

Measurements, in centimeters, of shoots of Phyllostachys nigra from May 3 to May 29, 1925

DATE	1		2		3		4		5		6	
	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN
May 3	7.5		9.8		14.3		.....		.....		.....	
4	10.0	2.5	12.8	3.0	18.0	3.7	1.4	....	.....	....	.....	....
5	12.4	2.4	15.3	2.5	22.0	4.0	2.4	1.0	.....	....	.....	....
6	15.3	2.9	18.9	3.6	27.6	5.6	4.0	1.6	.....	....	.....	....
7	23.2	7.9	28.3	9.4	41.3	13.7	7.7	3.7	.....	....	.....	....
8	31.8	8.6	38.5	10.2	56.0	14.7	12.0	4.3	9.0	....	11.0	....
9	39.2	7.4	47.4	8.9	64.8	8.8	15.7	3.7	11.8	2.8	15.2	4.2
10	48.1	8.9	57.7	10.3	78.0	13.2	20.2	4.5	15.0	3.2	19.8	4.6
11	61.0	12.9	70.0	12.3	91.2	13.2	27.6	7.4	19.6	4.6	26.0	6.2
12	74.0	13.0	87.6	17.6	106.0	14.8	37.0	9.4	26.7	7.1	34.2	8.2
13	96.8	22.8	103.0	15.4	131.0	25.0	51.0	14.0	38.5	11.8	49.6	15.4
14	124.5	27.7	138.8	35.8	161.0	30.0	70.3	19.3	53.6	15.1	67.2	19.6
15	150.5	26.0	165.5	26.7	190.0	29.0	88.0	17.7	68.0	14.4	86.5	19.3
16	179.2	28.7	196.7	31.2	213.5	23.5	109.5	21.5	88.0	20.0	107.0	20.5
17	200.0	20.8	220.2	23.5	235.0	21.5	125.0	15.5	101.0	13.0	124.2	17.2
18	226.7	26.7	248.5	28.3	249.8	14.8	149.0	24.0	121.5	20.5	150.1	24.9
19	256.0	29.3	273.7	25.2	268.0	18.2	183.5	34.5	154.7	33.2	182.6	32.5
20	282.4	26.4	301.5	27.8	274.0	6.0	221.4	37.9	195.5	40.8	216.5	33.9
21	297.0	14.6	317.0	15.5	277.7	3.7	242.0	20.6	219.0	23.5	232.0	15.5
22	319.5	22.5	334.0	17.0	278.2	0.5	270.5	28.5	250.7	31.7	259.5	27.5
23	329.0	9.5	335.0	1.0	280.0	2.4	292.6	22.1	272.5	21.8	275.8	16.3
24	.....	....	336.0	1.0	.....	....	309.0	16.4	286.5	14.0	279.0	3.2
25	.....	....	337.0	1.0	.....	....	318.0	9.0	292.0	5.5	284.0	5.0
26	.....	....	.....	....	.....	....	319.0	1.0	293.0	1.0	.....	....
27	.....	....	.....	....	.....	....	.....	....	.....	....	.....	....
28	.....	....	.....	....	.....	....	.....	....	.....	....	.....	....

TABLE 2—(Cont.)

Measurements, in centimeters, of shoots of Phyllostachys nigra from May 3 to May 29, 1925

DATE	7		8		9		10		MEAN DAILY TEMPERATURE	RELATIVE HUMIDITY	DAILY RAINFALL
	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN			
May 3	.....		.....		.....		.....		16.8	89.4	4.1
4	.....	....	.....	....	.....	....	.....	....	14.9	84.4	....
5	.....	....	.....	....	.....	....	.....	....	16.1	87.5	0.3
6	.....	....	.....	....	.....	....	.....	....	20.2	83.9	....
7	.....	....	.....	....	.....	....	.....	....	18.7	91.0	12.6
8	12.8	....	8.9	....	.....	....	.....	....	15.9	80.2	2.0
9	15.0	2.2	10.9	2.0	.....	....	.....	....	15.8	81.5	1.1
10	18.2	3.2	13.6	2.7	5.5	....	16.4	....	16.8	77.5	....
11	23.1	4.9	17.7	4.1	7.1	1.6	22.6	6.2	16.0	83.6	....
12	30.5	7.4	23.7	6.0	11.3	4.2	30.6	8.0	17.2	97.0	89.9
13	43.0	12.5	34.6	10.9	15.5	4.2	43.5	12.9	22.8	89.5	4.7
14	60.5	17.5	49.8	15.2	23.5	8.0	61.7	18.2	21.0	80.4	0.5
15	78.5	18.0	64.5	14.7	31.0	7.5	80.1	18.4	18.3	81.0	....
16	98.0	19.5	81.5	17.0	40.0	9.0	98.5	18.4	16.7	89.1	2.7
17	110.4	12.4	91.4	9.9	50.4	10.4	112.3	13.8	17.2	74.2	....
18	132.0	21.6	107.0	15.6	62.4	12.0	138.5	26.2	19.6	73.7	....
19	164.5	32.5	118.2	11.2	85.0	22.6	185.0	46.5	21.0	69.7	....
20	204.0	39.5	144.5	26.3	116.0	31.0	220.0	35.0	19.8	66.2	....
21	229.2	25.2	162.0	17.5	138.5	22.5	247.2	27.2	18.9	60.0	....
22	278.0	48.8	188.4	26.4	175.5	37.0	292.0	44.8	21.8	70.1	....
23	315.5	37.5	211.0	22.6	208.0	32.5	324.7	32.7	22.7	78.8	....
24	347.0	31.5	227.0	16.0	234.6	26.6	350.0	25.3	19.2	91.3	....
25	369.5	22.5	232.0	5.0	256.0	21.4	372.0	22.0	23.0	77.2	....
26	390.0*	30.5	237.0	5.0	271.8	15.8	390.0	18.0	20.2	92.2	4.9
27	.....	....	.....	....	280.0	8.2	393.0	3.0	20.6	90.2	0.2
28	.....	....	....	....	281.3	1.3	.....	....	21.8	80.6	....

TABLE 3

Measurements, in centimeters, of shoots of Phyllostachys nigra from April 21 to May 22, 1926

DATE	1		2		3		4		5		6	
	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN
Apr 21	4.0		.....		.....		.....		.....		.....	
22	5.0	1.0	.....	....	.....	....	.....	....	.....	....	.....	....
23	5.8	0.8	.....	....	.....	....	.....	....	.....	....	.....	....
24	6.8	1.0	.....	....	.....	....	.....	....	.....	....	.....	....
25	.....	....	.....	....	.....	....	.....	....	.....	....	.....	....
26	.....	....	.....	....	.....	....	.....	....	.....	....	.....	....
27	.....	....	.....	....	.....	....	.....	....	.....	....	.....	....
28	14.1	....	8.6	....	8.7	....	.....	....	.....	....	.....	....
29	16.9	2.8	10.2	1.6	10.7	2.0	7.3	....	5.7	....	6.5	....
30	20.1	3.2	12.8	2.6	12.5	1.8	10.2	2.9	8.4	2.7	8.6	2.1
May 1	25.7	5.6	16.4	3.6	16.2	3.7	12.8	2.6	11.2	2.8	11.4	2.8
2	35.8	10.1	22.0	5.6	22.0	5.8	17.6	4.8	17.0	5.8	16.5	5.1
3	49.5	13.7	30.1	8.1	34.1	12.1	24.5	6.9	23.7	6.7	23.7	7.2
4	69.5	20.0	44.0	13.9	45.7	11.6	34.3	9.8	36.5	12.8	34.9	11.2
5	88.0	18.5	60.8	16.8	63.0	17.3	48.7	14.4	51.1	14.6	48.8	13.9
6	118.0	30.0	84.0	23.2	88.3	25.3	70.0	21.3	71.5	20.4	69.6	20.8
7	138.0	20.0	99.6	15.3	106.6	18.3	86.0	16.0	86.5	15.0	84.7	15.1
8	168.7	30.7	124.9	25.3	130.3	23.7	110.2	24.2	110.5	24.0	106.6	21.9
9	209.9	41.2	159.0	34.1	167.7	37.4	140.5	30.3	136.7	26.2	137.7	31.1
10	240.7	30.8	189.6	30.6	200.5	32.8	166.3	25.8	161.9	25.2	165.0	27.3
11	267.0	26.3	227.0	37.4	240.5	40.0	200.4	34.1	192.6	30.7	198.5	33.5
12	293.0	26.0	272.5	45.5	290.0	49.5	229.5	29.1	234.3	41.7	241.5	43.0
13	305.6	12.6	301.8	29.3	318.4	28.4	268.2	38.7	258.0	23.7	267.0	25.5
14	313.5	7.9	330.2	28.4	347.5	29.1	301.0	32.8	287.4	29.4	295.0	28.0
15	320.0	6.5	351.0	20.5	367.0	19.5	327.0	26.0	308.0	20.6	311.5	16.5
16	326.0	6.0	367.5	16.5	383.6	16.6	350.0	23.0	322.0	14.0	326.0	14.5
17	328.0	2.0	383.0	15.5	398.3	14.7	369.4	19.4	338.0	16.0	338.0	12.0
18	331.4	3.4	400.5	17.5	410.0	11.7	394.5	25.1	356.0	18.0	355.7	17.7
19	.....	....	410.0	9.5	414.5	4.5	410.5	16.0	.....	....	358.3	2.6
20	.....	....	411.5	1.5	.....	....	419.0	8.5	.....	....	359.3	1.0
21	.....	....	413.0	1.5	.....	....	422.0	3.0	.....	....	.....	....

TABLE 3—(Cont.)

Measurements, in centimeters, of shoots of Phyllostachys nigra from April 21 to May 22, 1926

DATE	7		8		9		10		MEAN DAILY TEMPERATURE	RELATIVE HUMIDITY	DAILY RAINFALL
	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN			
Apr 21	.....		.....		.....		.....		12.6	57.6	....
22	.....	....	.....	....	.....	....	.....	....	12.5	86.8	21.5
23	.....	....	.....	....	.....	....	.....	....	15.1	91.0	0.2
24	.....	....	.....	....	.....	....	.....	....	12.6	89.0	....
25	.....	....	.....	....	.....	....	.....	....	16.0	70.0	....
26	.....	....	.....	....	.....	....	.....	....	16.4	62.9	....
27	.....	....	.....	....	.....	....	.....	....	14.7	75.7	2.1
28	.....	....	.....	....	.....	....	.....	....	14.0	80.2	....
29	9.6	....	.....	....	.....	....	.....	....	14.3	62.7	....
30	12.6	3.0	.....	....	.....	....	.....	....	15.6	63.2	....
May 1	16.7	4.1	21.8	....	11.0	....	11.0	....	18.3	73.4	....
2	24.0	7.3	30.3	8.5	15.6	4.6	14.9	3.9	19.4	81.7	....
3	34.2	10.2	43.3	13.0	22.2	6.6	20.4	5.5	21.5	84.2	....
4	49.9	15.7	61.8	18.5	32.7	19.5	29.3	8.9	20.5	84.3	....
5	68.3	18.4	81.2	19.4	45.3	12.6	40.6	11.3	21.3	87.2	4.7
6	94.4	26.1	107.6	26.6	64.3	19.0	58.9	18.3	17.4	78.9	0.5
7	108.8	14.4	125.5	17.7	78.0	13.7	71.6	12.7	18.8	57.5	....
8	137.2	26.4	157.8	32.3	99.5	21.5	92.5	20.9	19.8	58.0	....
9	167.8	30.6	198.2	40.4	127.8	28.3	121.0	28.5	18.6	81.0	2.0
10	195.0	27.2	235.7	37.5	152.5	24.7	144.5	23.5	20.2	89.7	0.8
11	228.0	33.0	275.0	39.3	183.1	30.6	178.5	34.0	21.6	75.3	....
12	265.0	37.0	316.0	41.0	224.7	41.6	221.0	42.5	16.9	92.5	15.0
13	285.5	20.8	336.3	20.3	252.7	28.0	254.2	33.2	18.8	79.1	....
14	305.5	19.7	352.3	16.0	286.5	33.8	291.2	37.0	17.8	67.8	....
15	320.0	14.5	366.0	13.7	312.2	25.7	320.6	29.4	15.6	74.6	....
16	330.0	10.0	374.0	8.0	334.4	22.2	346.0	25.4	16.1	76.8	....
17	342.0	12.0	385.0	11.0	354.5	20.1	368.2	22.2	18.7	80.6	....
18	349.6	7.6	385.4	0.4	377.5	23.0	396.5	28.3	22.4	77.0	....
19	.....	....	387.2	1.8	396.5	19.0	415.1	18.6	20.6	93.8	20.9
20	.....	....	.....	....	402.5	6.0	422.5	7.4	22.8	68.9	....
21	.....	....	.....	....	405.0	3.5	424.0	1.5	21.9	69.4	....

TABLE 4

Measurements, in centimeters, of shoots of Phyllostachys quadrangularis from October 6 to November 14, 1925

DATE	1		2		3		4		5		6		7	
	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN
Oct 6	63.2		29.4		20.0		19.5		16.7		56.5		.....	
7	73.5	10.3	34.3	4.9	22.0	2.0	22.9	3.4	17.8	1.1	68.5	12.0	12.0	....
8	86.0	12.5	41.9	7.6	25.0	3.0	25.6	2.7	19.8	2.0	80.0	11.5	13.7	1.7
9	99.2	13.2	50.1	8.2	29.5	4.5	30.2	4.6	23.0	3.2	94.0	14.0	15.8	2.1
10	107.0	7.8	60.0	9.9	34.5	5.0	35.0	4.8	25.4	2.4	104.5	10.5	18.0	2.2
11	116.0	9.0	68.8	8.8	40.0	5.5	40.6	5.6	28.8	3.4	115.0	10.5	18.8	0.8
12	122.9	6.9	82.5	13.7	47.5	7.5	48.0	7.4	33.8	5.0	125.0	10.0	21.0	2.2
13	134.0	11.1	95.5	13.0	57.0	9.5	59.0	11.0	40.0	6.2	133.9	8.9	24.3	3.3
14	143.3	9.3	108.7	13.2	68.0	11.0	70.4	11.4	48.3	8.3	141.0	7.1	28.0	3.7
15	151.5	8.2	118.8	10.1	78.9	10.9	81.8	11.4	57.4	9.1	146.4	5.4	32.0	4.0
16	157.7	6.2	127.5	8.7	91.0	12.1	92.5	10.7	67.5	10.1	150.7	4.3	37.0	5.0
17	163.0	5.3	135.0	7.5	102.0	11.0	103.8	11.3	77.0	9.5	153.5	2.8	42.2	5.2
18	167.2	4.2	142.5	7.5	114.0	12.0	115.0	11.2	88.6	11.6	156.5	3.0	50.2	8.0
19	171.5	4.3	150.3	7.8	127.0	13.0	127.0	12.0	103.0	14.4	158.5	2.0	60.6	10.4
20	173.5	2.0	155.3	5.0	135.5	8.5	133.5	4.5	110.3	7.3	159.5	1.0	69.8	9.2
21	175.3	1.8	158.6	3.3	141.5	6.0	136.0	4.5	115.2	4.9	160.3	0.8	76.7	6.9
22	177.0	1.7	162.2	3.6	147.3	5.8	139.5	3.5	120.6	5.4	161.0	0.7	85.1	8.4
23	178.7	1.7	165.5	3.3	154.0	6.7	143.2	3.7	126.9	6.3	162.0	1.0	95.5	10.4
24	180.2	1.5	169.2	3.7	160.5	6.5	145.7	2.5	132.0	5.1	162.4	0.4	108.0	12.5
25	181.2	1.0	171.0	1.8	166.0	5.5	147.5	1.8	135.8	3.8	163.1	0.7	119.0	11.0
26	182.1	0.9	172.6	1.6	169.7	3.7	149.2	1.7	139.8	4.0	163.4	0.3	129.2	10.2
27	183.0	0.9	174.0	1.4	173.2	3.5	152.0	2.8	143.7	3.9	163.6	0.2	141.3	12.1
28	184.0	1.0	176.2	2.2	177.5	4.3	152.7	0.7	147.0	3.3	164.2	1.4	153.4	12.1
29	184.5	0.5	178.0	1.8	179.2	1.7	152.9	0.2	149.8	2.8	164.3	0.1	164.5	11.1
30	184.9	0.4	178.5	0.5	182.0	2.8	153.0	0.1	151.5	1.7	164.6	0.3	170.2	5.7
31	185.8	0.9	179.0	0.5	182.1	0.1	153.3	0.5	152.7	....	165.2	....	177.1	....
Nov 1	186.1	0.3	179.7	0.7	185.0	2.9	154.3	0.8	153.9	1.2	165.3	0.1	182.0	4.9
2	186.3	0.2	180.1	0.4	185.8	0.8	155.0	0.7	155.0	1.1	.....	....	185.7	3.7
3	186.8	0.5	180.3	0.2	186.5	0.7	155.2	0.2	155.4	0.4	.....	....	187.6	1.9
4	.....	....	180.7	0.4	187.0	0.5	.....	....	156.0	0.6	165.5	0.2	189.7	2.1
5	187.3	0.5	181.0	0.3	.....	....	155.7	0.5	156.3	0.3	.....	....	191.0	1.3
6	187.7	0.4	181.5	0.5	187.2	0.2	.....	....	156.8	0.5	.....	....	192.5	0.5
7	188.0	0.3	.....	....	.....	....	156.1	0.4	.....	....	.....	....	192.3	0.8
8	188.5	0.5	182.0	0.5	188.2	1.0	156.3	0.2	157.5	0.7	165.7	0.2	193.2	0.9
9	188.7	0.2	.....	....	.....	....	157.0	0.7	158.2	0.7	166.0	0.3	193.9	0.7
10	.....	....	182.7	0.7	189.0	0.8	157.2	0.2	158.6	0.4	.....	....	195.0	1.1
11	189.0	0.3	183.0	0.3	189.2	0.2	.....	....	.....	....	166.5	0.5	195.5	0.5
12	189.2	0.2	.....	....	189.4	0.2	157.3	0.1	159.5	0.1	166.7	0.2	196.0	0.5
13	189.5	0.3	183.3	0.3	.....	....	157.5	0.2	.....	....	166.8	0.1	.....	....

TABLE 4—(Cont.)

Measurements, in centimeters, of shoots of Phyllostachys quadrangularis from October 6 to November 14, 1925

DATE	8		9		10		11		MEAN DAILY TEMPERATURE	RELATIVE HUMIDITY	DAILY RAINFALL
	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN			
Oct 6	.....		.....		.....		.....		19.8	74.7	...
7	12.2	....	16.1	....	.....	....	.....	....	18.2	78.0	...
8	14.0	1.8	18.6	2.5	36.5	....	.....	....	19.9	78.3	...
9	14.3	0.3	21.0	2.4	44.3	7.8	.....	.....	17.7	67.0	...
10	15.2	0.9	23.0	2.0	50.4	6.1	24.0	.....	15.1	66.2	...
11	15.6	0.4	25.8	2.8	56.5	6.1	28.1	4.1	16.4	71.8	...
12	16.0	0.4	30.0	4.2	66.5	10.0	32.7	4.6	17.2	78.2	...
13	17.1	1.1	35.0	5.0	77.0	10.5	39.8	7.1	16.9	74.6	...
14	18.2	1.1	43.0	8.0	87.8	10.8	47.7	7.9	16.7	75.4	...
15	19.7	1.5	49.7	6.7	97.8	10.0	56.3	8.6	16.5	75.4	...
16	20.5	0.8	57.5	7.8	107.9	10.1	65.5	9.2	16.1	72.0	...
17	.....	....	66.5	9.0	114.4	6.5	74.0	8.5	16.4	73.0	...
18	21.1	0.6	77.8	11.3	123.0	8.6	86.7	12.7	17.6	75.9	...
19	21.5	0.4	91.5	13.7	131.7	8.7	100.6	13.9	17.0	71.7	...
20	22.0	0.5	102.0	10.5	136.5	4.8	110.2	9.6	13.3	68.1	...
21	22.7	0.7	109.6	7.6	141.2	4.7	116.5	6.3	13.8	66.2	...
22	24.7	2.0	118.4	8.8	144.5	3.3	123.4	6.9	15.5	69.9	...
23	27.0	2.3	129.0	10.6	148.3	3.8	131.2	7.8	16.8	67.6	...
24	32.0	5.0	140.4	11.4	152.1	3.8	139.5	8.3	15.9	72.9	...
25	37.3	5.3	150.0	9.6	155.2	3.1	146.3	6.8	15.2	75.0	...
26	43.5	6.2	157.7	7.7	156.6	1.4	151.8	5.5	17.0	74.4	...
27	52.0	8.5	166.5	8.8	159.0	2.4	157.2	5.4	18.1	74.0	...
28	62.7	10.7	175.0	8.5	163.8	4.8	162.4	5.2	19.0	77.4	...
29	74.5	11.8	181.0	6.0	.....	....	165.8	3.4	16.2	79.7	...
30	80.2	5.7	184.0	3.0	.....	....	167.0	1.2	15.2	74.3	....
31	86.0	....	186.8	2.8	164.4	0.6	168.3	1.3	16.4	71.9	...
Nov 1	93.4	7.4	189.0	2.2	164.8	0.4	169.2	0.9	15.3	75.5	...
2	99.2	5.8	189.8	0.8	165.8	1.0	169.4	0.2	14.8	76.3	...
3	105.0	5.8	191.5	1.7	166.4	0.6	170.5	1.1	14.6	76.6	0.1
4	107.6	2.6	192.3	0.8	167.0	0.6	170.7	0.2	12.1	64.2	...
5	109.0	1.4	192.6	0.3	167.1	0.1	171.1	0.4	11.7	65.8	...
6	111.2	2.2	193.2	0.6	167.4	0.3	172.2	1.1	12.5	72.8	...
7	114.2	3.0	194.0	0.8	167.5	0.1	172.5	0.3	14.3	77.0	...
8	117.5	3.3	195.0	1.0	168.0	0.5	173.0	0.5	17.1	79.7	...
9	119.5	2.0	.....	....	.....	....	173.3	0.3	19.5	76.0	...
10	121.0	1.5	.....	....	168.5	0.5	174.0	0.7	16.5	90.7	4.8
11	122.5	1.5	196.2	1.2	169.1	0.6	.....	....	15.6	87.3	4.2
12	123.7	1.2	.....	....	169.9	0.8	174.3	0.3	12.4	91.8	25.1
13	124.5	0.8	196.7	0.1	.....	....	174.4	0.1	9.5	71.8	...

TABLE 5

Measurements, in centimeters, of shoots of Phyllostachys quadrangularis from October 20 to November 22, 1926

DATE	1		2		3		4		5		6		7	
	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN
Oct 20	14.4		33.5		.....		.....		.....		.....		.....	
21	16.2	1.8	36.6	3.1	29.2	....	.....	....	.....	....	.....	....	.....	....
22	19.0	2.8	43.5	6.9	33.5	4.3	.....	....	.....	....	.....	....	.....	....
23	22.2	3.2	51.0	7.5	40.0	6.5	.....	....	.....	....	.....	....	.....	....
24	25.0	2.8	57.1	6.1	45.7	5.7	.....	....	.....	....	.....	....	55.3	....
25	31.0	6.0	62.0	4.9	53.2	7.5	66.4	....	.....	....	.....	....	65.2	9.9
26	34.6	3.6	74.9	12.9	61.9	8.7	77.6	11.2	.....	....	19.8	....	76.5	11.3
27	42.7	8.1	87.1	12.2	75.2	13.3	87.7	10.1	.....	....	23.5	3.7	92.8	16.3
28	49.6	6.7	97.6	10.5	85.5	10.3	95.6	7.9	43.0	....	27.3	3.8	104.7	11.9
29	55.4	5.8	104.2	6.6	92.3	6.8	101.7	6.1	47.5	4.5	29.9	2.6	113.5	8.8
30	58.5	3.1	107.6	3.4	95.5	3.2	104.9	3.2	50.3	2.8	31.7	1.8	118.3	4.8
31	61.2	2.7	111.1	3.5	98.2	2.7	107.9	3.0	52.8	2.5	33.7	2.0	122.2	3.9
Nov 1	64.5	3.3	114.7	3.6	101.6	3.4	110.7	2.8	56.0	3.2	35.8	2.1	126.6	4.4
2	69.4	4.9	121.3	6.6	107.5	5.9	115.8	5.1	61.8	5.8	40.0	4.2	134.2	7.6
3	74.8	5.4	128.0	6.7	113.9	6.4	119.7	3.9	68.6	6.8	45.5	5.5	143.0	8.8
4	78.3	3.5	133.2	5.2	118.3	4.4	123.8	4.1	74.1	5.5	50.0	4.5	148.2	5.2
5	83.3	5.0	138.3	5.1	123.0	4.7	127.1	3.3	80.7	6.6	55.0	5.0	154.4	6.2
6	87.6	4.3	143.3	5.0	127.4	4.4	130.2	3.1	87.5	6.8	60.4	5.4	160.8	6.4
7	93.0	5.4	150.0	6.7	132.7	5.3	132.7	2.5	96.0	8.5	67.2	6.8	167.7	6.9
8	99.1	6.1	155.8	5.8	138.5	5.8	135.7	3.0	106.6	10.6	77.0	9.8	175.3	7.6
9	105.1	6.0	161.1	5.3	143.0	4.5	138.2	2.5	116.7	10.1	87.8	10.8	181.7	6.4
10	112.3	7.2	167.0	5.9	147.4	4.4	140.5	2.3	126.6	9.9	102.8	15.0	188.9	7.2
11	116.5	4.2	170.8	3.8	150.0	2.6	142.1	1.6	132.5	5.9	113.8	11.0	194.0	5.1
12	122.0	5.5	175.5	4.7	152.0	2.0	143.2	1.1	139.1	6.6	124.0	10.2	198.5	4.5
13	128.0	6.0	179.3	3.8	154.6	2.6	144.4	1.2	145.1	6.0	135.6	11.6	203.1	4.6
14	130.2	2.2	180.8	1.5	155.5	0.9	144.6	0.2	145.7	0.6	138.6	3.0	203.6	0.5
15	131.0	0.8	181.5	0.7	155.8	0.3	144.8	0.2	147.5	1.8	139.8	1.2	204.7	1.1
16	132.2	1.2	182.3	0.8	156.3	0.5	145.3	0.5	148.5	1.0	142.3	2.5	205.6	0.9
17	133.5	1.3	183.2	0.9	156.7	0.4	145.5	0.2	149.5	1.0	144.7	2.4	205.6	....
18	134.4	0.9	184.0	0.8	157.3	0.6	145.8	0.3	150.6	1.1	146.6	1.9	206.0	0.4
19	134.6	0.2	184.8	0.8	157.6	0.3	145.8	....	151.1	0.5	148.1	1.5	207.0	1.0
20	135.8	1.2	185.2	0.4	157.7	0.1	.....	....	151.7	0.6	149.2	1.1	207.0	....
21	136.5	0.7	185.7	0.5	157.8	0.1	.....	....	152.5	0.8	150.6	1.4	207.1	0.1

TABLE 5—(Cont.)

Measurements, in centimeters, of shoots of Phyllostachys quadrangularis from October 20 to November 22, 1926

DATE		8		9		10		11		12		MEAN DAILY TEMPERATURE	RELATIVE HUMIDITY	DAILY RAINFALL
		HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN	HEIGHT	GAIN			
Oct	20	.....		.....		.....		.....		10.5		12.2	72.9	....
	21	.....	....	15.4	....	16.3	....	8.8	....	11.8	1.3	14.4	78.3	...
	22	.....	....	17.4	2.0	18.0	1.7	10.0	1.2	13.4	1.6	16.8	78.9	...
	23	.....	....	20.0	2.6	20.4	2.4	11.0	1.0	15.5	2.1	14.4	78.8	...
	24	53.5	....	22.2	2.2	22.5	2.1	12.1	1.1	17.2	1.7	14.2	76.0	...
	25	63.2	9.7	25.4	3.2	25.5	3.0	13.2	1.1	20.4	3.2	16.3	77.8	...
	26	74.2	11.0	30.0	4.6	29.9	4.4	14.9	1.7	22.9	2.5	16.6	81.6	...
	27	89.0	14.8	37.0	7.0	36.7	6.8	18.8	3.9	27.4	4.5	15.9	91.8	5 1
	28	99.4	10.4	43.7	6.7	43.3	6.6	20.0	1.2	33.5	6.1	13.6	70.6	...
	29	107.3	7.9	48.7	5.0	48.1	4.8	21.7	1.7	37.2	3.7	9.9	54.9	...
	30	111.4	4.1	51.6	2.9	50.7	2.6	23.0	1.3	39.5	2.3	7.5	58.9	...
	31	114.0	2.6	54.6	3.0	53.7	3.0	24.2	1.2	41.5	2.0	8.4	70.4	...
Nov	1	117.2	3.2	57.8	3.2	56.8	3.1	25.8	1.6	44.4	2.9	11.4	78.1	...
	2	124.2	7.0	64.2	6.4	63.0	6.2	28.8	3.0	49.5	5.1	13.2	76.4	...
	3	130.6	6.4	72.0	7.8	70.0	7.0	32.7	3.9	55.5	6.0	10.6	87.7	1.5
	4	135.1	4.5	78.1	6.1	75.8	5.8	35.5	2.8	60.9	5.4	11.3	80.3	...
	5	140.2	5.1	85.3	7.2	82.5	6.7	39.3	3.8	66.8	5.9	12.4	75.2	...
	6	145.0	4.8	93.2	7.9	90.0	7.5	43.4	4.1	73.5	6.7	12.8	76.0	...
	7	151.0	6.0	103.0	9.8	98.6	8.6	49.0	5.6	82.1	8.6	15.4	78.4	...
	8	156.8	5.8	115.0	12.0	109.6	11.0	57.1	8.1	93.3	11.2	16.7	82.3	...
	9	162.1	5.3	127.1	12.1	121.3	11.7	66.4	9.3	105.5	12.2	16.7	89.5	1.5
	10	166.8	4.7	138.4	11.3	135.8	14.5	78.5	12.1	120.1	14.6	15.8	88.0	...
	11	169.7	2.9	143.3	4.9	144.0	8.2	88.8	10.3	130.5	10.4	16.9	87.8	...
	12	172.8	3.1	149.5	6.2	152.4	8.4	100.8	12.0	142.5	12.0	19.7	88.2	1.7
	13	174.7	1.9	156.6	7.1	162.2	9.8	111.6	10.8	156.0	13.5	15.1	90.1	...
	14	175.2	0.5	157.3	0.7	164.5	2.3	115.7	4.1	159.2	3.2	9.6	75.4	1.3
	15	175.8	0.6	158.0	0.7	165.7	1.2	118.5	2.8	161.0	1.8	9.8	73.7	0.7
	16	176.3	0.5	160.1	1.1	167.4	1.7	122.0	3.5	163.8	2.8	10.3	96.8	30.3
	17	176.9	0.6	160.7	0.6	168.5	1.1	125.1	3.1	165.9	2.1	11.4	85.6	7.2
	18	177.5	0.6	161.7	1.0	169.3	0.8	128.8	3.7	167.9	2.0	10.6	75.9	...
	19	178.0	0.5	162.4	0.7	170.1	0.8	131.3	2.5	170.0	2.1	9.0	77.5	...
	20	178.0	....	163.1	0.7	171.0	0.9	133.9	2.6	171.4	1.4	9.0	76.9	...
	21	178.5	0.5	164.2	1.1	172.0	1.0	137.0	3.1	173.6	2.2	12.4	84.4	3.9

A revision of the Plantago patagonica group of the United States and Canada

Ione Poe

Asa Gray (Syn. Fl. 2 : 391. 1878) treats this group as one species (*Plantago patagonica* Jacq.) with four varieties—*gnaphalioides*, *spinulosa*, *nuda*, and *aristata*. Miss Alida Cunningham (Proc. Indiana Acad. Sci. **1896:** 190-206) separates one species, *P. minima*, and refers all other plants to *P. patagonica* with five varieties, *lanatifolia* being the added one. Morris (Bull. Torrey Club **27:** 105-119. 1900; **28:** 112-122. 1901) divides the group into twenty-one species. One species, *P. Gooddingii* (Muhlenbergia **3:** 142. 1908), has been added since, making a total of twenty-two species. Since Morris' first paper so many species-names have been current as to be very confusing. It was because of inability to determine satisfactorily the plants collected in Southern California that this study was suggested to me by Dr. Philip A. Munz of Pomona College.

I wish to express my thanks to Dr. Munz for his help and encouragement and to Dr. Ivan M. Johnston of the Gray Herbarium for looking up material in herbarium and library. For this study I have had altogether some 1300 sheets, only a small portion of which can be cited in this paper. This material was loaned from the United States National Herbarium (US), Gray Herbarium of Harvard University (G), Missouri Botanical Garden (M), Rocky Mountain Herbarium of the University of Wyoming (W), Pomona College Herbarium (P), and the private herbarium of Mr. Frank Peirson of Pasadena (FP). To those in charge of these herbaria I express my appreciation of their kindness in making loans of their material.

It has been difficult to find diagnostic characters for this group. Some characters are so constant that they offer no variations of diagnostic importance. This is true of the corolla (except in size), stamens, pistils, capsule and number of seeds. On the other hand, some characters vary so much that it is impossible to make groupings with them as a basis. This is true of the size of the whole plant, the width and length of the leaves, and of the presence of denticulations on the leaves.

A leaf from any locality may have denticulations, yet not all the leaves of a collection, nor even all leaves of a given plant. Moreover, these denticulations occasionally occur in plants otherwise widely separated. Field studies have convinced me that many variations are due directly to environment. For example, plants growing in full sun tend to have shorter, more vigorous stems and wider leaves, yet bracts remain fairly constant. Seeds were sown of *P. Purshii* (*Munz 10493*, from Baldwin Lake, San Bernardino Mts., Calif.) some in dense shade, others in open sun. The first were exceedingly depauperate and weak, but kept the long linear bracts to a remarkable degree. Depauperate plants occur in most of the species and have sometimes been given varietal or even specific rank, but I have not given such recognition where these differences are evidently ecological. Furthermore, depauperate and typical flowers sometimes occur on the same plant. The diagnostic characters which have been found most usable are length and shape of bracts, color of dried plant, color and texture of seeds, shape of spike and size of corolla. An effort has also been made to get geographical entities, although sometimes not very clear demarcations of range have been possible.

A study of Jacquin's plate and description of the species *P. patagonica* (Jacq., Ic. Rar. *pl. 306*. 1781-93, and Jacq., Coll. 5. 1796) makes it seem different from any North American species. But in the Gray Herbarium are two sheets from Argentina (Ge eral Roca, *Fischer 6* and *Gilles*) which are very like our *P. Purshii* and, if really to be referred to *P. patagonica* make *P. Purshii* seem very close to the South American species. However, it hardly seems wise to take up the name *patagonica* for any of our northern plants without more abundant and authentic material than has been available for this study.

In the definition of the *patagonica* group I have followed Gray, *l. c.*, to a large extent. The plants treated are all native annuals with the flowers open over the mature capsule and with two cymbiform, deeply excavated seeds. However, the leaves are not always silky-pubescent or lanate.

KEY TO SPECIES AND VARIETIES

a. Bracts, at least some lower ones, two or more times as long as calyces.

b. Bracts all drying dark brown or black; plants of Mississippi Valley, Texas and eastern United States.

c. Bracts all conspicuous; corollas not conspicuous, lobes less than 3 mm. long.....1. *P. aristata*

c. Only a few lower bracts of each spike conspicuous; corollas conspicuous, lobes 3 mm. or more long.....4. *P. Helleri*

b Bracts all drying green to gray; plants of Mississippi Valley to southern California.

c. Bracts all conspicuous, aristate and usually all acute; plants from Mississippi River to Colorado, from Canada to Texas and New Mexico.....2a. *P. spinulosa* var. *typica*

c. Bracts of upper flowers of each spike inconspicuous and distinctly shorter than lower and more aristate ones, usually all blunt; plants from Utah and Arizona to the Colorado Desert of California.....2b. *P spinulosa* var. *oblonga*

a. Bracts not over two times as long as calyces.

b. Lowest bracts (including scarious margin if present) of each spike narrow at base, linear-subulate to narrowly lanceolate.

c. Flowers not conspicuously large, corolla-lobes less than 3 mm. long; seeds less than 3 mm. long; plants of the western half of the United States.

d. Bracts linear-subulate; leaves usually light green; range from Indiana south through Texas to southern California, from Minnesota west to Washington and Oregon.

e. Spikes with white-woolly pubescence; range same as *d* above.....3a. *P. Purshii* var. *typica*

e. Spikes with yellowish or fuscous pubescence, usually short cylindric; range from Utah and Arizona to the Colorado Desert of California.....2b. *P. spinulosa* var. *oblonga*

d. Bracts lanceolate (rarely linear-subulate); leaves usually dark bluish-green; plants of Arizona and New Mexico.....3b. *P. Purshii* var. *argyrea*

c. Flowers conspicuously large; corolla lobes 3 mm. or more long; seeds 3–4 mm. long; plants of Texas.....4. *P. Helleri*

b. Lowest bracts (including scarious margin) of each spike wide at base, broadly lanceolate to ovate, oblong or orbicular.

c. Seeds dull brown when mature, punctate; bracts not like sepals.

d. Spikes short-cylindrical or capitate, not over four times as long as wide; bracts scarious margined one third of length to whole length of rigid midrib; plants of California and Oregon.....5c. *P. Hookeriana* var. *californica*

d. Spikes long cylindrical, at least four times as long as wide; bracts scarious margined one half or less the length of the rigid midrib.

e. Leaves glabrous or glabrate, usually drying a dark brown; corolla lobes 2–4 mm. long; plants of northern Texas and Oklahoma to Arizona.....5b. *P. Hookeriana* var. *nuda*

e. Leaves villous or lanate; usually drying green; corolla lobes rarely over 2mm. long; plants of Texas.....5a. *P. Hookeriana* var. *typica*

c. Seeds reddish-yellow when mature, glossy; bracts nearly like sepals.

d. Plants not white-woolly; bracts with brown midribs (usually);

plants of coast, coast islands and upper San Joaquin Valley of California.....6a. *P. insularis* var. *typica*

d. Plants noticeably white-woolly; bracts with green midribs (usually); ranging from the Mohave and Colorado Deserts of California, to Arizona and Utah.....6b. *P. insularis* var. *fastigiata*

TREATMENT OF SPECIES

1. PLANTAGO ARISTATA Michx., Fl. Bor. Am. **1**: 95. 1803. *P. gnaphalioides* var. *aristata* Hook., Fl. Bor. Am. **2**: 124. 1840. *P. patagonica* var. *aristata* Gray, Man. ed. 2. 269. 1856; Cunningham, Proc. Indiana Acad. Sci. **1896**: 200. 1897 (in part). *P. aristata* Michx., Morris, Bull. Torrey Club **27**: 107. 1900. *P. Nuttallii* Rapin, Mem. Soc. Linn. Paris **6**: 470. 1827 (1828) according to Morris. *P. squarrosa* Nutt., Trans. Am. Phil. Soc. n. s. **5**: 178. 1837, not Murr., Comm. Goett. 38. *pl. 3*.1781, according to Morris. *P. filiformis* Dcne., ex DC., Prod. **13**: 714. 1852. *P. aristata Nuttallii* (Rapin) Morris, Bull. Torrey Club **27**: 108. 1900.

Plants drying a dark green; leaves entire, acute, callous-tipped, 50-200 mm. long, 3-8 mm. wide, glabrous to villous; scapes erect, surpassing leaves, 120-300 mm. long, glabrous to pubescent; spikes usually long cylindrical, 15-150 mm. long, 5 mm. wide (exclusive of bracts); bracts aristate, narrowly linear, 5-35 mm. long, 1 mm. wide, drying dark brown or black; calyx divisions spatulate-oblong, 2-4 mm. long, 0.5-1 mm. wide, glabrous to villous; corolla lobes white with brown spot at base of each, 2 mm. long, 1.5-2 mm. wide, stamens barely exserted, seeds dark brown, oblong, finely pitted, 2-3 mm. long.

Type locality: in meadows of Illinois. Representative material: TEXAS: San Patricio, *Berlandier*, May 1834 (M); Dallas, *Reverchon*, May 1901 (M).—OKLAHOMA: Shawneetown, McCurtain Co., *Houghton 3841* (M, P); Payne Co., *White*, June 1900 (M, W).—KANSAS: Riley Co., *Norton*, June 1895 (M, W).—NEBRASKA: Halsey, *Reverchon*, June 1904 (M).—SOUTH DAKOTA: Brookings, *Thornber*, June 1894 (M).—IOWA: Mt. Pleasant, *Ball 1582* (M); Ames, *Campbell*, July 1909 (M).—MISSOURI: St. Louis, *Eggert*, June 1874 (W); Courtney, Jackson Co., *Bush 385* (US, M); McDonald Co., *Bush*, July 1893 (M); Pilot Knob, *Pammel*, June 1888 (M); Willard, *Blankinship*, June 1919 (P).—ARKANSAS: Pine Bluff, Jefferson Co., *Eggert*, June 1898 (M).—LOUISIANA: Alexandria, *Ball 393* (US, M).—MISSISSIPPI: Natchez, *Shimek*, June 1898 (M).—ALABAMA: Birmingham, *Earle 2071* (US).—GEORGIA: Thompson, McDuffie Co., *Bartlett 1619* (P).—FLORIDA: Fort Myers, Lee Co., *Standley*, June 1916 (M).—SOUTH CAROLINA: Anderson, Anderson Co., *Davis 7707* (M).—NORTH CAROLINA: Roandale Farm, *Wetherby 71* (US).—TENNESSEE: Knoxville, *Ruth*, Aug. 1893 (M).—VIRGINIA: Suffolk,

Nansemond Co., *Heller*, June 1893 (W).—KENTUCKY: Lexington, *McFarland 62* (M).—ILLINOIS: Chicago, *Greenman*, June 1911 (M).—INDIANA: South Bend, *Clemens*, Aug. 1909 (P).—OHIO: Berea, *Ashcroft*, July 1897 (M).—MICHIGAN: Grand Haven, *Walter*, Sept. 1902 (US).—PENNSYLVANIA: Sayre, *Barbour, 726* (W).—MARYLAND: Hyattsville, *Dowell 6282* (M).—NEW JERSEY: Ocean Co., *Birdsall*, July 1890 (W).—NEW YORK: Bedford Park, *Wilson*, July 1899 (W).—MASSACHUSETTS: Wellesley, *Winslow*, June 1912 (M).—MAINE: North Berwick, *Parlin 973* (US).—VERMONT: Brandon, *Dutton*, Oct. 1912 (M).

The long bracts of this species, brown or black when dried, are the most conspicuous character. They distinguish *P. aristata* from all other species of the *patagonica* group.

Growing with the typical *P. aristata* is a depauperate form with filiform root, filiform leaves, smaller spikes and shorter bracts. These plants were made var. *Nuttallii* by Morris. I can not consider them as a variety, but merely an ecological form, occurring here and there throughout the range of the species. Representative material: OKLAHOMA: Stillwater, *Waugh 197* (M, US).—TEXAS: "a Bejar ad Rio Colorado," *Berlandier 1846*, type coll. *P. filiformis* (M); Houston, *Hall 399* (P, M).—IOWA: Van Wert, *Hitchcock*, July 1888 (M).—MISSOURI: Jefferson Co., *Eggert*, June 1892 (M).—ARKANSAS: Fayetteville, *Harvey*, *Arkansas Flora 55* (M).—GEORGIA: Warm Springs, *Tracy 8968* (US, M).—NORTH CAROLINA: Polk Co., *Churchill*, May 1899 (M).—TENNESSEE: Coffee Co., *Eggert*, June 1897.—ILLINOIS: Hancock Co., *Gates 8867* (M).—CONNECTICUT: Fairfield, *Eames*, Aug. 1895 (US).

Specimens showing the intergrades between the typical form and the depauperate form are: NORTH CAROLINA: Biltmore, June 1897 (M).—TEXAS: Dallas, *Reverchon*, April 1901 (M).—OHIO: Cleveland, *Stair*, July 1894 (M).—DISTRICT OF COLUMBIA: Eckington, *Painter*, June 1903 (M).

Two collections studied have the form and size of *P. aristata* but the bracts are not the typical dark brown or black color. They are: OKLAHOMA: Miami, *Stevens 2341* (M) and MISSOURI: Swan, *Bush 768* (M).

2. PLANTAGO SPINULOSA Dcne., ex DC., Prod. **13:** 713. 1852.

Plant erect, light green, leaves acute, callous-tipped, glabrate to villous, 25-150 mm. long, 1-4 mm. wide, scapes erect or ascending, pubescent to villous (sometimes glabrate), spikes short- to long-cylindrical, sometimes interrupted, 10-100 mm. long, bracts linear-subulate to aristate, slightly enlarged and sometimes scarious-margined at base, 6-17 mm. long, villous, calyx divisions linear-oblong, scarious-margined, 2-3 mm. long, villous, corolla lobes white, with brown spot at base of each, 1-1.5 mm. long, pyxis 2-3 mm. long, seeds dark brown, oblong, finely pitted, 1.5-2 mm. long.

2a. P. SPINULOSA var. **typica** n. nom. *P. spinulosa* Dcne., *l. c.;* Morris, Bull. Torrey Club **27:** 109. 1900 (in part); **28:** 116.

1901. *P. patagonica* var. *spinulosa* Gray, Man., ed. 2.269. 1856. *P. verticillata* Morris, Bull. Torrey Club **28**:117. 1901.

Spikes cylindrical, slender, sometimes interrupted, bracts all aristate and conspicuous and usually acute.

Type locality: Texas. Representative material: CANADA: Cypress Hills, Northwest Territory, *Macoun*, Aug. 1880 (US); Milk River, Alberta, *Macoun 12898* (US).—MONTANA: Bozeman, *Blankinship 420* (US. W, P).—WYOMING; Laramie, *Nelson 136* (US); Worland, *Buffum*, June 1909 (W), in part.—SOUTH DAKOTA: Crook, Harding Co., *Visher 314* (W); Fort Pierre, *Geyer 275* (US, M).—NORTH DAKOTA: Glen Ullin, *Bergman 2421* (M).—COLORADO: Denver, *Jones 343* (P).—KANSAS: Cowley Co., *White 60* (M).—OKLAHOMA: Fort Sill, *Clemens 11787* (W) in part; Ingersoll, *Bush 1508* (M).—TEXAS: Eastern Texas, *Wright*, in 1848–49, photograph of type of *P. spinulosa* (M); Kerrville, *Heller 1769*, type collection of *P. verticillata* (M); Amarillo, *Wooton*, July 1914 (US).—NEW MEXICO: Clovis, *Wooton*, July 1914 (US); *Wright 1439* (G).

This variety is like *P. aristata* in the long aristate bracts, but is at once distinguished from it by the light green color and the more western range. I have not seen the type sheet of *P. verticillata*, but a cotype annotated by Morris (*Heller 1769*). Because it was impossible to distinguish the plants on this sheet from ordinary material of *P. spinulosa* var. *typica*, *P. verticillata* seems best reduced to synonomy. Although the type comes from Texas, plants with the same interrupted form of spike have been seen from widely diverse regions such as Colorado, Denver, *Jones 343* (P) and Montana, Bozeman, *Blankinship 420* (P). This interrupted spike is evidently an ecological form, apparently due to shade.

2b. P. SPINULOSA var. **oblonga** (Morris) comb. nov.—*P. spinulosa* of Morris, Bull. Torrey Club **27**: 109. 1900 (for plants of southern California, Arizona and Utah). *P. patagonica* var. *aristata* of Cunningham, Proc. Indiana Acad. Sci. **1896**: 200. 1897 (for plants of southern California). *P. oblonga* Morris, Bull. Torrey Club **28**:119. 1901. *P. ignota* Morris, *l. c.*

Spikes usually short-cylindrical, compact; usually all bracts blunt, upper bracts inconspicuous and distinctly shorter than the lower and more conspicuous, more aristate ones.

Type locality: Colorado Desert, San Diego Co., California. Representative material: CALIFORNIA: Colorado Desert, *Orcutt* in 1870, type collection of *P. oblonga* (US); Banning, *Orcutt* in 1891 (M).—UTAH: Silver Reef, *Jones 5163ag* (P, US).—ARIZONA: Wilmot, *Thornber 527* (US, M); Camp Grant, *Palmer* in 1867 (M); Tucson, *Beard* in 1911 (M); Tucson Mts., *Thornber 398* (US, M, P); Ehrenberg, *Palmer 309* (M); Mescal Mts., *Jones* in 1890 (P); Santa Rita Forest Reserve, *Griffiths 4159* (M); Laosa, *Griffiths 3597* (M); Coyote to Santa Rosa, *Griffiths 3997* (M).—NEW MEXICO: Albuquerque, *Harwood* (M).

This variety, in length of bracts, stands between *P. spinulosa* var. *typica* and *P. Purshii* var. *typica*, but the brownish color of the spikes places it with

P. spinulosa. I have not seen the type of *P. ignota*, but I have seen material annotated by Morris as *P. ignota*, and I cannot distinguish it from *P. oblonga*; the two having the same structure and range.

3. PLANTAGO PURSHII R. & S., Syst. **3**: 120. Mar. 20, 1818.

Plant erect; leaves entire, acute, callous-tipped, 30-130 mm. long, 1-4 mm. wide, glabrate to lanate; scapes erect or ascending, 40-110 mm. long, pubescent to villous; spikes usually long cylindrical, 20-120 mm. long; bracts linear-subulate to lanceolate, not more than twice the length of the calyces, sometimes slightly scarious-margined at the base, 3-8 mm. long, villous; calyx divisions oval or ovate, 2-3 mm. long, villous; corolla lobes white with brown spot at base of each, 1-2 mm. long; stamens barely exserted or on long capillary filaments; seeds light or dark brown, oblong, finely pitted, 1.5-2 mm. long.

3a. P. PURSHII var. **typica** n. nom.—*P. Purshii* R. & S., *l. c. P. Lagopus* Pursh, Fl. **1**: 99. 1814 (not *P. Lagopus* L., Sp. Pl. 114. 1753). *P. gnaphalioides* Nutt., Gen. **1**: 100. May 27, 1818. *P. curta* Engelm., ex DC., Prod. **13**: 713. 1852. *P. patagonica* var. *gnaphalioides* Gray, Man., ed. 2.269. 1856. *P. picta* Morris, Bull. Torrey Club **28**:118. 1901 (not *P. picta* Colenso, Trans. New Zeal. Inst. **22**:481. 1890). *P. xerodea* Morris, Bull. Torrey Club **36**: 515. 1909.

Leaves villous to white-wooly; spikes usually long cylindrical, dense, villous to wooly; bracts linear-subulate, rigid, of same length or sometimes twice as long as calyces, sometimes slightly scarious-margined; seeds 1.5-2 mm. long.

Type locality: in dry situations on the banks of the Missouri.

This variety has a larger natural range than any other corresponding entity within the *patagonica* group, and it not surpising that there is considerable variation. Typical material runs as follows: NORTH DAKOTA: Leeds, Benson Co., *Lunell* in 1900 (W); Dickinson, *Holgate* in 1908 (G).—SOUTH DAKOTA: Fall River Co., *Visher 2584* (W); Fort Pierre, *Geyer* in 1839 (M); Brookings, *Thornber* in 1894 (M, G).—MINNESOTA: Pipestone, *Munzel* in 1896 (W); St. Paul, *Churchill* in 1912 (G).—IOWA: Moscow, *Somes 3236* (US).—MISSOURI: Allenton, *Kellogg* in 1886 (M); Courtney, *Bush 2585* (M, G); Sheffield, *Bush 2097* (M).—ILLINOIS: Peoria, *McDonald* in 1900 (W), in 1904 (G).—INDIANA: South Bend, *Clemens* in 1909 (P).—NEBRASKA: *Knight 774* (W); Lincoln, *Smith* in 1890 (M).—KANSAS: Andale, *Poole 283* (G); Riley Co., *Norton 418* (W, M, G).—OKLAHOMA: Ft. Gibson, *Engelmann?* in 1835, photograph of type of *P. curta* at Mus. Paris (P); Shattuck, Ellis Co., *Clifton 3141* (G); Fort Sill, *Clemens 11788* (W); Limestone Gap, *Buller 11268* (M).—COLORADO: Manitou, *Clements and Clements* in 1903 (M, G); Paradox, Montrose Co., *Walker*

83 (W, M, G); Larimer Co., *Baker 8777* (P).—WYOMING: Halleck Canyon, Albany Co., *Nelson 7450* (P, G, M); Powder River, Natrona Co., *Nelson 9370* (W, P, M, G); Newcastle, *Nelson 8442* (W); Pine Bluffs, *Nelson 3512* (P); Platte River, *Nelson 3052* (W).—MONTANA: Flathead Lake, *Clemens* in 1908 (G); Bozeman, *Blankinship 422* (W, M, P); Wreck Creek, Sweet Grass Co., *Eggleston 7967* (US).—CANADA: Milk River, Alberta, *Macoun 12899* (G); between Kettle and Columbian Rivers, *Macoun 67889* (P, M, G); Okanagon Lake, British Columbia, *Macoun* in 1889 (M); Medicine Hat, Assiniboia, *Macoun 5860* (G).—IDAHO: Pocatello, *Nelson and Macbride 1398* (W, M P, G); Boise, *Clark 120* (W, M, G); St. Anthony, *Merrill and Wilcox 829* (W, G); Coeur D'Alene Mts., *Leiberg 1598* (W); Clearwater River, Nez Perces Co., *Sandberg 267* (P, M, G).—WASHINGTON: Waitsburg, *Horner* in 1897 (G); Grand Dalles, *Westgate 3973* (US); Spokane, *Turesson* in 1912 (W) in part.—OREGON: Wallowa Co., *Sheldon 8118* (M); Jackson Co., *Hammond 205* (M); Dalles, Wasco Co., *Heller 10092* (G, M).—UTAH: Logan, Cache Co., *Smith 1731* (W); Green River, *Jones* in 1890 (P); Salt Lake City, *Garrett 1160* (W, G); Peterson, *Pammel and Blackwood 3890* (M, G).—NEW MEXICO: Organ Mts., Dona Ana Co., *Wooton* in 1905 (P, W); Farmington, San Juan Co., *Standley 6916* (US); Santa Fe, *Heller and Heller 3720* (M); Sandia Mts. *Ellis* in 1914 (M); Silver City, *Eastwood 8420* (G).—TEXAS: El Paso, *Jones 3707* (P 68923); Dallas, *Bush 632* (M); Midland, *Tracy* in 1902 (G).—ARIZONA: Laguna Canyon, Painted Desert, *Clute 32* (M, G); Flaggstaff, *MacDougal 220* (W, G); Santa Rita Forest Reserve, *Griffiths 4170* (M).

Growing with the usual form of *P. Purshii* var. *typica* is a depauperate form with smaller root, narrower, shorter leaves, and smaller spikes. As in the case of *P. aristata*, I can not consider this as a variety but merely an ecological form, occurring here and there throughout the range of var. *typica*. Depauperate material seen: NORTH DAKOTA: Leeds, *Lunell*, July 1899 (G).—SOUTH DAKOTA: Fort Pierre, *Hayden* in 1853–4 (M), in part.—COLORADO: Morrison, *Smith* in 1898 (M); Mancos, *Baker Earle and Tracy 809* (P, W, G).—IDAHO: Shoshone Falls, *Bennitt 159* (W); Blackfoot, *Palmer 251* (G).—WASHINGTON: Spokane, *Turesson* in 1912 (W), in part.—UTAH: Kanab, *Jones 5286y* (P).—WYOMING: Worland, *Buffum*, June 1909 (W) in part.—NEW MEXICO: Albuquerque, *Kammerer 53* (M); Aztec, *Baker 611* (M, P).—TEXAS: El Paso, *Thurber 182* (G).

The depauperate form of spike is even found growing on the same plant with the usual form, as evidenced by: INDIAN TERRITORY: Sapulpa, *Bush 467* (M).

There seems to be a tendency, in a large part of the range, toward longer bracts, thus approaching *P. spinulosa* var. *oblonga* in length of bracts, but not in shape of spike, nor general habit, nor range. Long bracted material studied: COLORADO: Fort Collins, *Crandall and Cowen* in 1896 (M); Manitou, *Clements and Clements* in 1903 (W); Paradox, Montrose Co., *Walker 83* (P).—WYOMING: Natrona Co., *Goodding 235* (M); Halleck Canon, Albany Co., *Nelson 7450* (W).—WASHINGTON: Douglas Co., *Sandberg and Leiberg 278* (M, G).—OREGON: Wilson Co., *Sandberg and Leiberg* in 1893 (M).—MONTANA: Ravalli, *Jones*, July 1909 (P).—NEW MEXICO: Cliff, Grant Co., *Metcalfe 205* (W).—SOUTH DAKOTA: Fort Pierre, *Hayden* in 1853–4 (M), in part.

I have seen two sheets of var. *typica* from Maine: North Berwick, *Parlin 1491* (G) and North Berwick in 1903 (G). The first was collected in a "newly seeded field" and the second was marked "wool waste" so that they are probably both artificially introduced.

Some plants from southern California, Utah, Nevada and Arizona are quite atypical in their thick short spikes, but they seem to belong to the *Purshii* var. *typica* group because of the whitish pubescence of the spikes and the absence of any proper differentiating characters. These plants, among which are those called *P. picta* by Morris, seem to form an intermediate group between *P. spinulosa* and *P. Purshii*. Atypical material studied: CALIFORNIA: Mouth of Santa Ana Canyon, *Parish 2643*, type collection of *P. picta* and *P. xerodea* (US); Julian, *Keck and McCully* in 1925 (P); Baldwin Lake, San Bernardino Mts., *Peirson 1180* (FP), *Munz 10493* (P); Providence Mts., *Munz and Harwood 3459* (P); Hesperia, *Munz 10827* (P); Kramer, *Craig Newsom and Hilend* in 1927 (P); between Mojave River and Rabbit Springs, *Parish 4902* (P, US), *4912* (P).—NEVADA: Meadow Valley Wash, *Jones*, April 1904 (P).—UTAH: St. George, *Goodding 808* (W).—ARIZONA: Hillside, *Jones*, May 1903 (P); Skull Valley, *Jones*, May 1903 (P).

3b. P. PURSHII var. **argyrea** (Morris) comb. nov.—*P. argyrea* Morris, Bull. Torrey Club **27**:111. 1900.

Leaves drying dark green, pubescent or canescent with white hairs, spikes long cylindrical, sometimes interrupted, not woolly; bracts of same length as calyces or shorter, lanceolate (rarely linear-subulate), usually narrowly scarious-margined; seeds about 2 mm. long.

Type locality: Castle Creek, Arizona. Material examined: ARIZONA: Castle Creek, *Toumey 355c*, type collection of *P. argyrea* (US); Tunitcha Mts., *Standley 7532* (US); Flagstaff, *Pearson 7* (US); Rim of Grand Canyon, *Hitchcock* in 1915 (US); Gallinas River, *Eggleston 5965* (US); Walnut Canon, *Mac Dougal 335* (US, G); Taylor, *Hough 77* (US); White Mts., *Griffiths 5372* (M).—NEW MEXICO: Mogollon Mts., Socorro Co., *Metcalfe 424* (G, W, M, P); Datil National Forest, *Rogers 8* (US).

This variety is closely related to *P. Purshii* var. *typica*, but is separated from it because of the color and pubescence of the leaves and spikes and the shape of the bracts.

Two specimens studied had the dark green leaves of var. *argyrea*, but the white-woolly spikes of var. *typica*. They were from Prescott, Arizona, *Hitchcock* in 1915 (US) and Navajo Indian Reservation, Carrizo Mts., Arizona, *Standley 7480* (US).

4. PLANTAGO HELLERI Small, Bull. N. Y. Bot. Gard. 1: 288. 1899.—Morris, Bull. Torrey Club **27**: 111. 1900.

Plants drying dark green; leaves entire, acute, callous-tipped, 50-130 mm. long, 2-6 mm. wide; scapes erect, villous; spikes short cylindrical, dense, 10-35 mm. long, bracts linear-

subulate, sometimes with narrow scarious-margin at base, lowest ones 4-9 mm. long, usually exceeding the calyces, upper ones shorter, equaling or shorter than calyces, calyx-divisions oval or oblong, with scarious margin wider than midrib, 3-4 mm. long; corolla lobes white, with brown spot at base of each, orbicular-ovate or sub-orbicular, 3-4 mm. long, 3 mm. wide; stamens barely exserted, seeds dark brown, oblong, finely pitted, 3-4 mm. long, 1.5-2 mm. wide.

Type locality: Kerrville, Kerr Co., Texas. Material examined: TEXAS: Kerrville, Kerr Co., *Heller 1649*, type collection of *P. Helleri* (P, US, M, G); Weatherford, *Tracy 7984* (US, G); San Antonio, *Slater* in 1918 (US); San Angelo, Tom Green Co., *Reverchon 3940* (US, M, G); Gillespie Co., *Jermy* (US), *207* (M); Temple, *Pace* in 1904 (US); Comanche Spring, New Braunfels, etc., *Lindheimer 1098* (US, M, G); Austin, *Hall 398* (US, M, G) Spofford, *Trelease 102* (M).—NEW MEXICO: *Wright* in 1851–52, No. *1437* (M, G), No. *1436* (M).

This species is conspicuous because of its large flowers and seeds. In shape of bract it is closely related to *P. Purshii* var. *typica*. In range it seems to be confined to Texas, although it may extend into Mexico. The one collection that has been available from New Mexico is of doubtful locality and may actually have been collected in Texas.

5. PLANTAGO HOOKERIANA F. & M., Ind. Sem. Petrop. 39. 1838.

Leaves filiform to narrowly lanceolate, entire or with small scattered denticulations, callous-tipped or truncate, 30-120 mm. long, glabrous to lanate, scapes erect or asecnding, 40-300 mm. long, glabrate to pubescent; spikes capitate or cylindric, 5-60 mm. long, two to many flowered, bracts wide at base, scarious-margined one third of length to whole length of midrib, all as short or shorter than calyces, glabrate to villous; calyx divisions oblong, 3 mm. long; corolla lobes white with brown spot at base of each or brown strips the whole length of each, 1-4 mm. long; stamens barely exserted or on long capillary filaments; seeds dull brown, finely pitted.

5a. P. HOOKERIANA var. **typica** n. nom.—*P. Hookeriana* F. & M., *l. c.* *P. patagonica* var. *lanatifolia* Coult. & Fish., Bot. Gaz. **18**:303.1893. *P. lanatifolia* (Coult. & Fish.) Small, Bull. Torrey Club **27**: 114.1900. *P. inflexa* Morris, Bull. Torrey Club **27**:113.1900.

Leaves villous or lanate, usually drying green; spikes long cylindrical; four times longer than wide; bracts scarious-margined one half of length of midrib or less; corolla lobes 2 mm. or less long.

Type locality: Texas. Material examined: TEXAS: *Lindheimer 163*, type collection of *P. inflexa* (G, M); Corpus Christi, *Heller 1392* (US, M, P, G); Torecillas, *Griffiths 6425* (M); Laredo, *Eggert*, April 1901 (M); San Antonio, *Schulz 423* (US); Victoria, *Eggert* April 1900 (M); Milano, *Palmer 11656* (M); Hearne, *Reverchon 3942* (US, M, G); Somerville, *Palmer 11700* (M); Dallas, *Reverchon*, April 1905 (M); Palestine, *Eggert*, June 1899 (M); Southwestern Texas, *Palmer 410* (US); El Paso, *Rose 11696* (US), *Jones 3707* (W, P 68922 and 68920); Valley of Rio Grande below Donana, *Emory 706a* (US). Type material of *P. Hookeriana* and *P. lanatifolia* has not been available, but the descriptions and much material from the region convince me of their identity.

It may seem unreasonable to put such forms as those from Milano, *Palmer 11656* (M), and Somerville, *Palmer 11700* (M), with those from El Paso, *Jones 3707* (P), and Laredo, *Eggert* April 1901 (M), but when the intermediate forms such as plants from Torrecillas, *Griffiths 6425* (M), and Victoria, *Eggert*, April 1900 (M), are considered, it becomes impossible to draw a line of demarcation between the tall erect forms and the spreading ones.

One specimen seen approaches *P. Purshii* in shape of bract but not in pubescence of spike. It is from Corpus Christi, *Orcutt 5917* (M).

5b. P. HOOKERIANA var. **nuda** (Gray) comb. nov.—*P. Wrightiana* Dcne., ex. DC., Prod. **13**:712.1852. Morris, Bull. Torrey Club **27**:112.1900. *P. patagonica* var. *nuda* Gray, Man., ed. 2.269.1856, for Texas material.

Leaves glabrous or glabrate, usually drying dark brown; spikes long cylindrical, four times as long as wide; corolla lobes 2-4 mm. long.

Type locality: Texas. Material examined: ARIZONA: Phoenix, *Wooton* in 1911 (US); Williams, *Griffiths 4875* (M).—OKLAHOMA: Cache, *Stevens 1322* (US, M, G); Fort Sill, *Clemens 11789* (W).—TEXAS: *Wright* in 1848, type collection of *P. Wrightiana* (G); *Lindheimer 511*, in 1846 (M, G); Weatherford, *Tracy 7984* (US, G); Abilene, *Eggert*, June 1900 (M); Comanche Spring, New Braunfels, etc., *Lindheimer 1100* (M, G); Colorado, *Eggert*, June 1900 (M); Gillespie Co., *Jermy 204* (US, M); Austin, *Hall 397* (P, US, M, G); Troupe, *Reverchon 3212* (M); Tarrant Co., *Ruth 117* (G).

This variety is conspicuous in its glabrous or glabrate leaves which caused Gray to give it the name *nuda*.

One depauperate collection studied has shorter, narrower leaves, finer peduncles, and smaller spikes than the typical plants of this variety. It is: Gillespie Co., Texas, *Jermy 209* (M, G in part).

Some plants have thicker more nearly capitate spikes than the typical plants. Such plants are: Prescott, Arizona, *Griffiths 7343* (M); Galveston Island, *Tharp 2941* (M); Weatherford, Texas, *Tracy 7984* (M).

Some plants have longer, more linear lower bracts than the typical ones, but have glabrate leaves and narrower spikes than *P. Helleri*. Such plants are: Austin, Texas, *Tharp 735* (US); San Marcos, Texas, *Fisher 68* (US).

5c. P. HOOKERIANA var. **californica** (Greene) comb. nov. —*P. patagonica* var. *californica* Greene, Man. Bay Reg. 236. 1894 (not *P. californica* Greene, Bull. Calif. Acad. Sci. **1**:123. 1885). Apparently *P. patagonica* var. *nuda* of Watson, Bot. Calif. **2**:478.1880 (for plants of California). *P. patagonica* var. *nuda* of Cunningham, Proc. Indiana Acad. Sci. **1896**:201.1897. *P. erecta* Morris, Bull. Torrey Club **27**:118.1900. *P. dura* Morris, Bull. Torrey Club **27**:113.1900. *P. speciosa* Morris, Bull. Torrey Club **28**:121.1901. *P. obversa* Morris, *l. c.* *P. tetrantha* Morris, Bull. Torrey Club **27**:119.1900.

Spikes short cylindrical or capitate, not over four times as long as wide; bracts scarious-margined one half the length of the midrib or more; corolla lobes 1-2 mm. long.

Type locality: California (Bay Region); type not designated. Material examined: CALIFORNIA: San Clemente Island, *Munz 6752* (P); Santa Catalina Island, *Grant 1000* (US, W, M, G); La Jolla, San Diego Co., *Clements 66* (M, G); Del Mar, *Angier 21*, type collection of *P. obversa* (M); Fallbrook, *Jones 3117* in March 1882 (M, US, P); Pala, *Munz 10359* (P); San Diego, *Brandegee 1632* (M, W, P, G); Pasadena, *Oleson* in 1907 (W); Azusa, *Grinnell* in 1906 (US); Claremont, *Baker 5255* (P); San Bernardino Valley, *Parish 335* (US), *5179* (W); Riverside, *Griffiths* in 1905 (US); Elsinore, *Robinson and Crocker* in 1916 (P); Laguna, Orange Co., *Munz 2212* (P); Sierra Canyon, Santa Ana Mts., *Munz and Harwood 3753* (P); San Buenaventura, *Brewer 230* (US); Lompoc, Santa Barbara Co., *Munz 10261* (P); San Luis Obispo, *Wooton* in 1913 (US); San Luis Obispo Co., *Miles* in 1886 (G); Coalinga, Fresno Co., *Munz 9173* (P); Keene Station, *Heller 7819* (M, G); North side of Tehachapi Pass, *Munz 8937* (P); Monterey Bay, *Heller 6653* (M, US, W, P, G); Cypress Point, *Eastwood 107* (M, G); Lindsay, Tulare Co., *Munz 9075* (P); Sequoia National Forest, *Jardine 133* (US); Stanford University, Santa Clara Co., *Baker 523* (W, P, M, G); Los Banos, Merced Co., *Wooton 1912* (US); Stoney Creek, Amador Co., *Hansen 2066* (M, US); Mt. Hood, *Heller 5167* (M, W, G, US); Bodega Point, *Eastwood 4827* (G); San Francisco, *Heller 6623* (P, M, W, G); Byron Springs, Contra Costa Co., *Eastwood 3802* (US, M, G); Berkeley Hills, *Millikan 66* (W); Mt. Diablo, *Baker 2828* (P); San Bruno Hills, Mateo Co., *Elmer 4795* (M, US, P); Vallejo, Solano Co., *Jones*251* (G); Marysville Buttes, *Heller 7582* (M, US, G); Napa Valley, *Thurber* in 1852 (G); Williams, Colusa Co., *Ferris 496* (P, M); Clear Creek, Butte Co., *Heller 5526* (W, M, US, G); Chico Creek, *Heller 12668* (US, M, G); Auburn, Plumas Co., *Ames* in 1891 (G); Rawhide Hill, Tuolumne Co., *Ferris 1478* (P); Humboldt Bay, *Chandler 1137* (US, M, G) McCloud's Fork, Shasta Co., *Smith 119* (G).—OREGON: Grant's Pass, *Howell* in 1884 (US), *Prescott* in 1912 (G); Coos Co., *House 5018* (US).

The variety *californica* is the characteristic *Plantago* of coastal and valley regions of California. It commonly has bracts with scarious margins the whole

length of the midrib, but so many times the midrib extends beyond the margin, that it is necessary to make the definition of the variety more inclusive than that of Morris' *P. erecta*, and to include several of Morris' species. Of these type material has not been available for *P. speciosa* or *P. dura*, but many sheets so designated by Morris have been studied. Morris' *P. erecta* is simply a new name for Greene's var. *californica*.

The depauperate plants of this variety are small in different ways. Some have filiform leaves and fewer flowers per spike. Examples are: Pomona, *Munz, Street and Williams 2403* (P); Oakland, *Mann* (G); La Jolla, *Clements and Clements 67* (G, M); Torrey Pines, *Peirson 4498* (FP), in part. Others have shorter pedicels and smaller spikes, making a more compact plant, as San Diego, *Peirson 3378* (FP), in part; San Diego, *Brandegee 1650* (P, G); Port Orford, Oregon, *Peck 9056* (G, M). *P. tetrantha* Morris is a depauperate form of this variety. Material examined: Santa Lucia Mts., *Plaskett 55*, type collection (G, US).

Several sheets have the characteristics of this variety except in shape of spikes, which are longer in proportion to the width than in the usual plants. Material examined: Del Mar, *Clements and Clements 68* (G); Antioch, *Baker 2803* (P); San Gabriel Mts., *Peirson 2747* (FP); Santa Catalina Island, *Schumaker* (G).

6. PLANTAGO INSULARIS Eastwood, PROC. California Acad. Sci. BOT. III.1:112.1898.

Leaves entire, acute, 25-100 mm. long, villous to lanate; scapes erect or ascending, surpassing the leaves, 25-160 mm. long, pubescent to villous, pubescence heavier just below the spikes; spikes capitate to short-cylindric, 5-25 mm. long; bracts ovate to orbicular, scarious with green or brown rigid midrib, as long as calyces or slightly shorter, glabrous to villous on midrib; calyx-divisions ovate or obovate, midribs green or brown, glabrate to villous; corolla lobes with brown spot at base of each or brown strips the whole length of each; seeds glossy and comparatively smooth, reddish-yellow when mature.

6a. P. INSULARIS var. **typica** n. nom.— *P. insularis* Eastwood, *l. c.* Jepson, Man. Fl. Pl. California 956.1925. *P. brunnea* Morris, Bull. Torrey Club **27**:115.1900.

Plants not noticeably white-woolly; bracts usually with brown midribs; plants of coast, coast islands and upper San Joaquin Valley of California.

Type locality: San Nicolas Island, seashore flats. Material examined: CALIFORNIA: Avalon, Santa Catalina Island, *Trask*, March 1898 (US, M); Santa Catalina Island, *Nuttall* in 1920 (P); San Clemente Island, *Wooton* in 1912 (US); San Nicolas Island, *Trask*, April 1897, type collection of *P. insularis* (US, M); San Diego, *Brandegee 1659* (US, M, W, P); Laguna, Orange Co., *Peirson 4668* (P, FP); Santa Barbara, *Eastwood 137* (US, M, G); Ojai,

Ventura Co., *Peckham* in 1866 (US); Oil City, Kern Co., *Heller 7589* (US, M, G); Maricopa Hills, Kern Co., *Eastwood 3270* (G, US).

One sheet of plants from San Clemente Island, *Peirson 3427* (FP), is more woolly than typical plants of this variety. Another from San Nicolas Island, *Trask 63* (G), is more woolly than the coastal plants and does not have such brown bracts. I have not seen the type of *P. brunnea*, but do not hesitate to reduce it to synonymy, from the description.

6b. P. INSULARIS var. FASTIGIATA (Morris) Jepson, Man. Fl. Pl. California 956.1925. *P. fastigiata* Morris, Bull. Torrey Club **27**:116.1900. *P. minima* Cunningham, Proc. Ind. Acad. Sci. **1896**:202.1897. Not *P. minima* DC., Fl. Fr. **3**:408.1805. Not *P. minima* Less., in Barneoud, Monog. Plantag. 41.1845. *P. scarioas* Morris, Bull. Torrey Club **27**:117.1900. *P. Gooddingii* Nelson & Kennedy, Muhlenbergia **3**:142.1908. *P. insularis* var. *scariosa* Jepson, Man. Fl. Pl. California 956.1925.

Plants noticeably white-woolly; bracts with usually green midribs; plants of Mohave and Colorado Deserts of California, of Nevada, of Arizona and of Utah.

Type locality: Tucson, Arizona. Material examined: ARIZONA: Tucson, *Toumey 355a*, type collection of *P. fastigiata* (US); *Griffiths 3528* (M), *Jones* May 1890 (P), *Lloyd* in 1907 (G); Beaverdam, *Jones 5024* (US, M, P); Yucca *Wooton* in 1912 (US); Santa Rita Forest Reserve, *Griffiths 4160* (M); Tucson Mts., *Griffiths 3495* (M); Yuma, *Goldman 1074* (US), *Jones*, April 1906 (P); Parker, *Wooton* in 1913 (US); Congress Junction, *Jones*, May 1903 (P); Tempe, *Ganong and Blaschka* in 1901 (US, G).—NEVADA: Lincoln Co., *Mills 10* (US); Moapa, *Goodding 2198* (W, M, G), *Kennedy 1070*, type collection of *P. Gooddingii* (W); Rioville, Colorado River, *Goodding 808a* (W); Good Springs, *Jones*, May 1905 (P).—UTAH: St. George, *Jones 1625* (P).—CALIFORNIA: Panamint Valley, *Coville and Funston 678* (US, M, G); Panamint Mts., *Hall and Chandler 7053* (P); Randsburg, Kern Co., *Heller 7694* (US, M, G); Colorado Desert, *Orcutt* in 1890 (M); Yaqui Wells, San Diego Co., *Eastwood 2720* (M, G); Imperial, *Wooton* in 1912 (US); Mecca, *Spencer* in 1922 (P, G); west of Yuma, *Jones*, April 1906 (P); Palm Springs, *Spencer 1487* (P, G); Dos Palmos Spring, *Munz 9969* (P); Chuckwalla Mts., *Munz and Keck 4879* (P); Fort Mohave, San Bernardino Co., *Cooper* in 1861 (US); Barstow, *Parish 9269* (M); Turtle Mts., *Munz and Harwood 3501* (P); Needles, *Munz and Harwood 3608* (W, P); Hesperia, *Munz 2609* (P); Kelso, *Jones*, May 1906 (P); Darwin, *Jones*, April 1897 (US, M, P).

The variety *fastigiata* is the characteristic *Plantago* of the desert regions of Arizona and southern California.

One sheet studied has unusually long, loose spikes, but otherwise is like the typical form. It is from Rioville, Nevada, *Goodding 808a* (W) in part. Another has long, loose spikes and

curved bracts. It is from Palm Canyon, California *Johnston* in 1917 (P).

No type is designated for Cunningham's *P. minima* or Morris' *P. scariosa*, which is a new name for *P. minima*, but I have seen material cited as *P. minima* by Cunningham and annotated as *P. scariosa* by Morris, and I cannot separate it even varietally from var. *fastigiata*.

POMONA COLLEGE,
CLAREMONT, CALIFORNIA

INDEX TO AMERICAN BOTANICAL LITERATURE

1923-1928

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